

2014

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Carpenter, Tim E.; Coggins, Victor L.; McCarthy, Clinton; O'Brien, Chans S.; O'Brien, Joshua M.; and Schommer, Timothy J., "A spatial risk assessment of bighorn sheep extirpation by grazing domestic sheep on public lands" (2014). *USDA Forest Service / UNL Faculty Publications*. 265.

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A spatial risk assessment of bighorn sheep extirpation by grazing domestic sheep on public lands



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ARTICLE INFO

Keywords:

Bighorn sheep
Epidemic simulation model
Viability analysis
Wildlife disease
Wildlife–livestock interface

ABSTRACT

Bighorn sheep currently occupy just 30% of their historic distribution, and persist in populations less than 5% as abundant overall as their early 19th century counterparts. Present-day recovery of bighorn sheep populations is in large part limited by periodic outbreaks of respiratory disease, which can be transmitted to bighorn sheep via contact with domestic sheep grazing in their vicinity. In order to assess the viability of bighorn sheep populations on the Payette National Forest (PNF) under several alternative proposals for domestic sheep grazing, we developed a series of interlinked models. Using telemetry and habitat data, we characterized herd home ranges and foray movements of bighorn sheep from their home ranges. Combining foray model movement estimates with known domestic sheep grazing areas (allotments), a Risk of Contact Model estimated bighorn sheep contact rates with domestic sheep allotments. Finally, we used demographic and epidemiologic data to construct population and disease transmission models (Disease Model), which we used to estimate bighorn sheep persistence under each alternative grazing scenario. Depending on the probability of disease transmission following interspecies contact, extirpation probabilities for the seven bighorn sheep herds examined here ranged from 20% to 100%. The Disease Model allowed us to assess the probabilities that varied domestic sheep management scenarios would support persistent populations of free-ranging bighorn sheep.

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1. Introduction

Prior to the mid-1800s, bighorn sheep (*Ovis canadensis*) were abundant and widely distributed throughout the

western United States. North American populations are estimated to have numbered between 1.5 and 2 million sheep (Buechner, 1960; Queen et al., 1994). Large declines in the species' abundance and distribution occurred during the late 1800s and early 1900s as a result of overharvest, habitat loss, and both forage competition and disease transmission from domestic livestock (Goodson, 1982; Valdez and Krausman, 1999). Unlike other ungulate species whose populations declined during the same period and then rebounded, bighorn sheep populations have seen limited

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recovery due largely to recurrent herd-level outbreaks of respiratory disease.

Bighorn sheep are highly susceptible to several diseases carried by closely related domestic sheep (Jessup, 1985). The disease-causing organisms most commonly associated with die-offs of free-ranging bighorn sheep are *Mycoplasma ovipneumoniae* (Besser et al., 2012a) and pathogenic strains of bacteria in several species formerly classified as members of the genus *Pasteurella*. These same strains are typically present in domestic sheep, who carry them without suffering significant deleterious effects (Miller, 2001; Dassanayake et al., 2009; Lawrence et al., 2010). Pen experiments indicate that direct contact between domestic sheep and bighorn sheep result in a high likelihood of disease transmission to bighorn sheep, which are lethal to the latter species (Onderka et al., 1988; Foreyt, 1994; Foreyt and Silflow, 1996; Lawrence et al., 2010; Besser et al., 2012b). In addition, numerous reports of pneumonia outbreaks following contact with domestic sheep indicate that contact poses a risk to free-ranging bighorn sheep herds (Foreyt and Jessup, 1982; Goodson, 1982; Coggins, 1988; George et al., 2008). While some debate has surrounded the idea that disease transmission from domestic sheep to bighorn sheep has triggered die-offs of wild bighorn sheep populations, the preponderance of relevant scientific literature supports the hypothesis that there is a significant risk resulting from interspecies contact that warrants consideration by managers.

In 2005, the Chief of the United States Forest Service (USFS) directed the Payette National Forest (PNF) to analyze bighorn sheep viability on the PNF in light of the known potential for impacts of disease transmission arising from grazing of domestic sheep in proximity to bighorn sheep (details in Forest Service (2010)). Following the Chief's

direction, we developed two linked models to estimate the probability of bighorn sheep population persistence under several potential management alternatives, which differed in the amount and distribution of domestic sheep grazing permitted on the PNF. The 'Risk of Contact Model' – described in full detail elsewhere (O'Brien et al., in press; USDA Forest Service, 2010) and briefly here – was designed to estimate the contact rate between bighorn sheep and active (sheep present) domestic sheep allotments. The 'Disease Model' and the subject of this article, models the population consequences of disease transmission from domestic sheep to bighorn sheep. Outputs from these models were used to describe current conditions and to make predictions for the future survival of the bighorn sheep on the PNF under a range of management alternatives.

2. Materials and methods

2.1. Bighorn sheep study population background

Two broadly delineated Rocky Mountain bighorn sheep (*O. c. canadensis*) metapopulations currently occur on the PNF, one within the Hells Canyon of the Snake River and the other among the Salmon River Mountains (USDA Forest Service, 2003) (Fig. 1). As suitable habitat connects most of these populations, this may historically have functioned as one metapopulation. Although Hells Canyon and its surrounding mountains may have once been home to more than 10,000 bighorn sheep, by the mid-1940s, bighorn sheep had been extirpated from the area (HCBSRC, 2005). Reintroduction efforts began in 1971 from a number of source herds in the western United States and Canada, and by 2004, 474 bighorn sheep had been translocated into Hells Canyon (HCBSRC, 2005). By 2005, despite

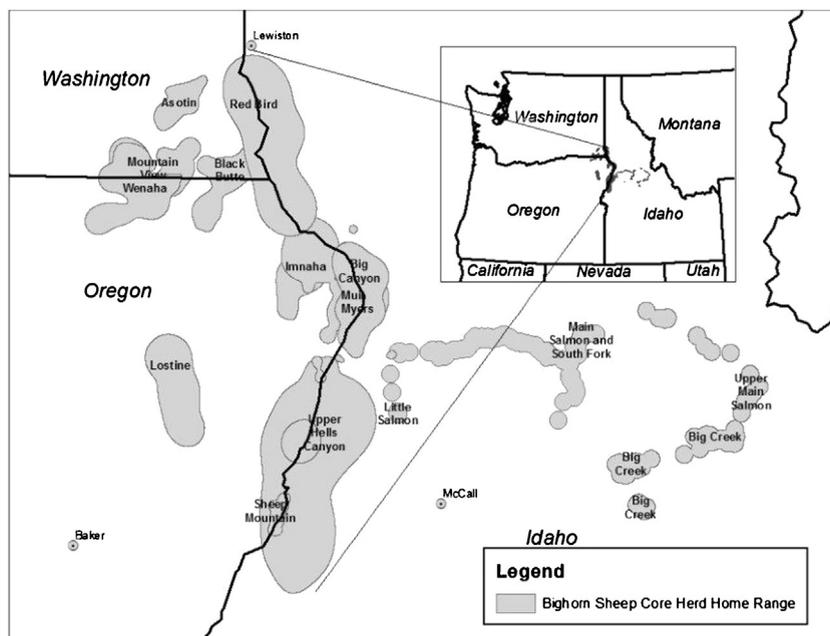


Fig. 1. Map of core herd home ranges of 12 Hells Canyon and 3 Salmon River bighorn sheep herds and 1 Area of Concern (Little Salmon) in the northwestern United States.

sustaining seven die-offs in the previous 35 years, the Hells Canyon metapopulation contained 875 animals in 12 herds (HCBSRC, 1997, 2005).

Despite experiencing periodic die-offs since at least the 1870s, the Salmon River metapopulation was never extirpated (Smith, 1954; Towell and Geist, 1999). Further, no introductions of bighorn sheep have been made into this native population (IDFG, 2010). Hence it is a high priority for conservation in Idaho. Recent winter population surveys document at least 704 bighorn sheep along the South Fork and main fork Salmon River canyons and their surrounding drainages (IDFG, 2010). Bighorn sheep in the parts where this metapopulation overlaps the PNF were assigned to three overlapping populations, the Main Salmon and South Fork, Upper Main Salmon, and Big Creek populations. At the time of this study, these three populations contained 483 animals. Bighorn sheep have occasionally been observed in one other area, the Little Salmon River. Animals observed along the Little Salmon River are treated as a small satellite population or “Area of Concern,” which is demographically linked to the nearby Main Salmon River population.

2.2. Models

For this analysis, we constructed two models: a Risk of Contact Model and the Disease Model presented here. Risk of contact between bighorn sheep and domestic sheep allotments was estimated using three linked analyses, which focused, respectively, on bighorn sheep habitat selection, identification of population core herd home range (CHHR) boundaries, and foray behavior. These analyses are described in detail elsewhere (O'Brien et al., in press; USDA, 2010) but will also be presented here in less detail. We constructed the Disease Model based on demographic and epidemiologic input specifications.

2.2.1. Risk of Contact Model

A ‘source habitat’ model, adapted from an expert-opinion based model produced for the Hells Canyon subpopulations by the Hells Canyon Bighorn Sheep Restoration Committee (HCBSRC, 1997), was used to identify areas of habitat considered suitable for use by bighorn sheep. That model was in turn based on work by Smith et al. (1991), Gudorf et al. (1996), and Sappington et al. (2007), whose research quantified bighorn sheep’s strong preference for areas close to steep, rugged terrain into which they can flee for safety. In addition, we followed guidelines by Schirokauer (1996) to identify areas that are open enough and that provided sufficient forage to be used as habitat by bighorn sheep. We modeled winter (November–April) source habitat as a subset of summer (May–October) source habitat, by adding an additional restriction that, above 4500 ft, winter source habitat only occurs on slopes with some south-facing component and which were estimated to be snow free in at least 3 of 7 winters.

Next, we used telemetry and observational data, to identify a CHHR for each of 15 herd groups and one Area of Concern in and around the PNF. As a first step, we computed a utilization distribution (a density surface representing an animal’s probability of occupying each point in space) for

each animal from which at least 20 telemetry points had been collected between 1997 and 2008. Following general recommendations in Laver and Kelly (2008), our home range estimation employed a bivariate kernel-based estimator (rather than, e.g., a minimum convex polygon or ellipse-based estimator) with a bandwidth estimated using the “reference” bandwidth estimator of Worton (1989). Individual-level utilization distributions for all animals in a herd were then combined by averaging to create a surface raster representing the utilization density of the herd as a whole. The home range modeling was completed with Home Range Extension version 1.1 for ArcGIS (Rodgers et al., 2007). The CHHR was defined as the isopleth (or contour) containing 95% of the utilization density.

To complete the Risk of Contact Model, we performed a foray analysis. A foray is any short-term movement of an animal away from and back to its herd’s CHHR (Singer et al., 2001). Forays are important, because they can put bighorn sheep at risk of contact with domestic sheep, even when those domestic sheep are located outside of bighorn sheep CHHRs (Gross et al., 2000; Singer et al., 2000). We modeled the annual probability and rates of contact with domestic sheep allotments as a function of the number of bighorn sheep in a herd and of the size, distance, and habitat composition of the allotment from the CHHR.

2.2.2. Disease Model

We developed the bighorn sheep Disease Model to relate expected contact and subsequent disease outbreak rates to longer-term probabilities of population extirpation. The model allowed for disease transmission from domestic sheep to bighorn sheep, and then to other adjacent, susceptible bighorn sheep herds. Although only some bighorn sheep herds in the Hells Canyon metapopulation overlap the PNF, they were all included in the model. In addition, we used the Disease Model to examine the cumulative effects of grazing domestic sheep grazing at several locations inside and outside the PNF boundaries, and their influence on bighorn sheep population persistence.

We constructed the Disease Model using a commercially available spreadsheet, Excel (Microsoft Corp., Redmond, WA), and made it probabilistic (stochastic), using a commercially available spreadsheet add-in, @RISK (Palisade Corp., Cornell, NY). Model outputs collected for each of the 15 bighorn sheep herds and one Area of Concern included distributions of annual population numbers, expected disease-return intervals (years between outbreaks), and probabilities of herd extirpation within 100 years.

2.2.3. Demographic input specifications

Initial herd population sizes – Population estimates for the 15 herds and one Area of Concern were based on data collected between 2007 and 2009 by the Idaho Department of Fish and Game, Oregon Department of Fish and Game, Washington Department of Fish and Wildlife, and Salmon River Bighorn Sheep Project (administered by the Nez Perce Tribe). For each herd, the most recently recorded population estimate was treated as the current population size. Herds (including the single Area of Concern) ranged in size from four to 210 animals. The 12 Hells Canyon herds collectively contained 665 individuals, and the three Salmon

River herds and single Area of Concern contained 487 individuals for a total of 1152 in all the modeled herds.

Population growth – We modeled population dynamics of healthy herds (i.e. those without respiratory disease) using a discrete logistic growth model, with the additional inclusion of a minimum population size (the non-viable number or NVN), below which a herd is bound to inexorably decline. The population in the current model year, N_{t+1} , given the population in the previous year, N_t , is given by the equations

$$N_{t+1} = N_t + rN_t \left(\frac{K - N_t}{K} \right), \quad \text{if } N_t \geq \text{NVN}, \quad (1)$$

$$N_{t+1} = N_t - N_t D, \quad \text{if } N_t < \text{NVN}, \quad (2)$$

where r is the intrinsic growth rate, D is the annual rate of decline for herds below the NVN, and K is the herd's estimated carrying capacity.

Our estimates of intrinsic growth rates, r , were based on data collected from 16 translocated Rocky Mountain bighorn sheep populations in Colorado, whose maximum annual growth rates ranged between 0.05 and 0.26 (McCarty and Miller, 1998). The Disease Model sampled maximum growth rates for each herd from a normal distribution (mean = 0.136, standard deviation = 0.057) fitted to the estimates of McCarty and Miller (1998).

For each herd, we took K (which ranged among herds from 34 to 975 individuals) to be 175% of the largest population count record for that herd since the 1970s (Hells Canyon herds) or the 1980s (Salmon River herds). Based on research showing that bighorn sheep herds whose populations decline below a critical value are unlikely to recover (and often decline to extinction) (Singer et al., 2000, 2001), we used an NVN of 30 individuals and an associated negative growth rate of -16% .

2.2.4. Epidemiologic Input Specifications

We used the following epidemiologic inputs to simulate the adverse effects of disease in bighorn sheep populations: initial herd infection status; bighorn sheep herd-to-herd transmission probability; domestic sheep-to-bighorn sheep transmission probability; disease outbreak impact; extended infectious duration; initial disease outbreak impact; and extended disease outbreak impact.

Initial herd infection status – For purposes of the model, we assumed that, initially, no bighorn sheep and all domestic sheep herds were infected with a pneumonia-causing pathogen.

Bighorn sheep herd-to-herd transmission probability – Using results obtained from the habitat, CHHR and foray analyses, we first constructed a matrix composed of the annual probabilities (p_{ij}) that an individual animal from herd j would foray to and make effective contact (i.e. a contact that resulting in disease transmission) with at least one individual in herd i .

Scaling up to the herd-level probability of transmission, we took the probability, P , of transmission to a susceptible bighorn sheep herd from an infected bighorn sheep herd to be given by

$$P_{ij} = 1 - q_{ij}^{C_j}, \quad (3)$$

where $q_{ij} = 1 - p_{ij}$ is the probability that susceptible herd i will avoid effective contact from one infected individual from herd j , and C_j is the number of infectious individuals in herd j (Abbey, 1952).

To compute the probability of infection from any one of n different infected bighorn sheep herds, P_i , we extended Eq. (3) as follows:

$$P_i = 1 - q_{i1}^{C_1} \dots q_{in}^{C_n}, \quad (4)$$

where q_{ij} is the probability that the susceptible bighorn sheep herd i will avoid effective contact with one infectious individual from herd j , and C_j is the number of infectious individuals in herd j .

Domestic sheep-to-bighorn sheep transmission probability – The model breaks the sequence of events by which a disease outbreak results from contact between a foraging bighorn sheep and a domestic sheep allotment into two groups of steps. First, to reach an occupied allotment, a bighorn sheep must leave its CHHR, travel far enough from it to reach the allotment, and intersect the allotment (rather than some other area at a similar distance from the CHHR). The Risk of Contact Model is used to estimate the seasonal probability (k) that an individual bighorn sheep will foray from its CHHR and make contact with an occupied domestic sheep allotment. This probability depends on which PNF domestic sheep allotments are left open to grazing, and so varies among different alternative management scenarios.

The second step estimates the compound probability that a foraging bighorn sheep, having reached an allotment, will make contact with an infectious domestic sheep, contract the disease, return to its CHHR, and initiate an outbreak. We performed a sensitivity analysis on this parameter to account for its uncertainty, and estimated the probability of an effective contact and subsequent herd-level outbreak, given cohabitation to be 5%, 25%, 50%, 75% and 100%, which permitted us to evaluate the assumption that the number of contacts to an allotment that will on average result in one disease outbreak in a given bighorn sheep herd ranges from 1 to 20. Multiplying this probability by k gave the seasonal probability that an individual bighorn sheep would foray from its CHHR, make effective contact with an infectious domestic sheep, and then initiate a die-off on its return to its CHHR.

We used computations similar to those presented in the previous section to scale up from the seasonal probability that one individual would cause an outbreak to the seasonal herd-level probability of an outbreak.

Disease transmission probability for disease transmission among combined bighorn sheep or domestic sheep-to-bighorn sheep – This probability depends on bighorn sheep herd size, bighorn sheep movements, and current herd infection status of contacted bighorn herds. The probability a herd becomes infected in the current year depends on the probability of the herd *not* avoiding effective contact with infected animals from either a bighorn or domestic sheep herd in the previous year.

Extended infectious duration – When a herd becomes infected, the animals in it typically remain infectious for more than 1 year. Besser et al. (2012b) and Foreyt (1990) document that disease perturbations can affect lamb recruitment for several years following a severe

population declines resulting from disease epizootics. Based on their work, we assumed the infectious duration followed a uniform distribution from 1 to 4 years.

Initial disease outbreak impact – Respiratory disease outbreaks in bighorn sheep herds typically manifest as an all-age die-off, followed by several years of reduced or zero lamb recruitment. To estimate mortality during the initial all-age die-off, we used observations from pneumonia outbreaks in seven Hells Canyon herds (Coggins, 1988; Cassirer et al., 1996; HCBSRC, 1997). Observed mortalities in these seven outbreaks were, respectively, 33%, 50%, 65%, 69%, 75%, 80% and 80%, and mortality from an outbreak in the Disease Model was sampled from a discrete distribution made up of those observed values.

Extended disease outbreak impact – We represented the reduced lamb recruitment that typically follows an all-age die-off as an extended period of depressed population growth in a diseased bighorn sheep herd. Based on observations reported in a variety of infected herds, we sampled the post-outbreak duration of reduced lamb recruitment from a uniform distribution from 4 to 10 years, including the initial year of infection (Coggins, 1988; Foreyt, 1990; McCarty and Miller, 1998; Gross et al., 2000; Monello et al., 2001; Miller et al., 2000; Cassirer et al., 2001; Miller, 2001; Cassirer and Sinclair, 2007; George et al., 2008). During this period of reduced lamb recruitment, the diseased herd's annual population growth rate was sampled from a uniform distribution ranging from –13% to 0%.

2.2.5. Stochastic features of the models

The Risk of Contact and Disease Models were both stochastic to reflect components of uncertainty and variability. We used Monte Carlo sampling to produce one thousand replicates 100-year long replicates of each simulated scenario.

2.3. Analysis and outputs

The PNF examined 17 alternative management scenarios (each differing in the areas left open to domestic sheep). To simplify matters, we here present just one of those, the alternative that would have maintained the *status quo* by leaving all then-grazed allotments open to continued grazing. Outputs reported here are the probabilities of extirpation for each of the seven bighorn sheep herds located on, or adjacent to, the PNF, as these populations are directly influenced by National Forest's management decisions.

3. Results

3.1. Contact risk

Bighorn sheep source habitat is contiguous and distributed across the PNF. We identified 369,641 acres of summer source habitat and 156,919 acres of winter source habitat representing, respectively, 15.4% and 6.5% of the PNF. If no restrictions were placed on domestic sheep grazing in the PNF, 100,310 acres of suitable rangeland habitat would be available to the domestic sheep, resulting in two bighorn sheep herds with 6.0% and 15.8%, respectively,

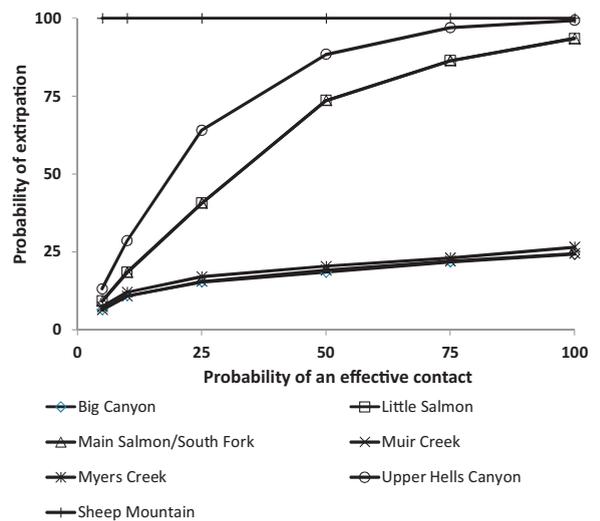


Fig. 2. Probability of extirpation of seven bighorn sheep populations on, and adjacent to, the Payette National Forest (PNF) during 100 years vs. alternative probabilities of effective contact.

of their CHHRs overlapped by occupied domestic sheep allotments. Home ranges of six other bighorn sheep herds would be located within 12 km of occupied allotments and two more would be located within 35–38 km. By examining telemetry data, we found 6.5% (14/215) of the ewes and 28.8% (30/104) of the rams having forays during the summer months and 12.9% (28/217) and 34.9% (38/109) of the ewes and rams, respectively, having forays during the winter months in a given year. When converted to animal-years with at least one foray, we found that in any one summer, when domestic sheep allotments on the PNF were most likely to be active, 14.1% of the rams, and 1.5% of the ewes forayed beyond the 95% isopleth of the CHHRs.

Half of all ram forays reached at least 10 km from the CHHR, 25% of reached at least 16 km, and the longest observed ram foray took the animal at least 35 km from its CHHR. Based on results obtained from the habitat, CHRR and foray analyses, we estimated if there were no allotment restrictions, a mean of 1.33 contacts per year between domestic sheep and bighorn sheep in the seven herds on or adjacent to the PNF.

3.2. Disease risk

We used the number of annual contacts generated from the contact model as an input for the disease transmission model. We compared six alternative effective contact probabilities (i.e. the probability that contact with an allotment would result in a bighorn sheep disease outbreak): 5%, 10%, 25%, 50%, 75% and 100% and here present estimated extirpation probabilities for seven bighorn sheep herds on or adjacent to the PNF (Fig. 2). Due to its small initial population of 10 individuals, well below the 30 animal NVN, the Sheep Mountain herd is extirpated with 100% probability under all scenarios. For the six other herds, the estimated extirpation probability ranged from 20% to 53% (given a 5% effective contact probability) or from 61% to 100% (given a 100% effective contact probability).

4. Discussion

We reported the probability of extirpation for seven herds on, or adjacent to, the PNF was high, between 20% and 100%, if all domestic sheep allotments were allowed to persist in the PNF, and would likely result in extreme population declines in an already fragile population. The findings are consistent with the conclusions of researchers in USDA Forest Service Region 2 (the “Rocky Mountain” region), who identified the risk of disease outbreaks resulting from contact with domestic sheep and goats as the most significant threat facing bighorns in both Region 2 and across their range (Beecham et al., 2007). A long history of large-scale, rapid, all-age die-offs in bighorn sheep has been documented across Canada and the US, and many die-offs appear to have been preceded by contact with domestic sheep or goats (Besser et al., 2012b; Shackleton et al., 1999). Bighorn sheep die-offs are associated with infection by *Mannheimia haemolytica*, which has been reported as the primary cause for bighorn sheep population declines throughout North America (Garde et al., 2005). Recent literature also suggests that *M. ovipneumoniae* plays an important role in susceptibility of bighorn sheep to pneumonia pathogens (Besser et al., 2012a). Several major disease-related die-offs in bighorn sheep have been reported in herds on or near the PNF. At least seven population die-offs have been reported since reintroductions were initiated in Hells Canyon (HCB SRC, 1997). *Pasteurella multocida* was associated with a major die-off in Hells Canyon in 1995 to 1996 (Frank et al., 2004). Over 300 Hells Canyon bighorn sheep died of pasteurellosis during this outbreak, which may have been initiated by contact with one domestic goat (Cassirer et al., 1996; Coggins, 2002).

Based on data from seven suspected pneumonia outbreaks (Coggins, 1988; Cassirer et al., 1996; HCB SRC, 1997), we estimated that mortality from a disease outbreak would range from 33% to 80%. Others have reported similar ranges of mortality from outbreaks of pneumonia. In a review of 48 public records of pneumonia epidemics Singer et al. (2000) reported highly variable mortalities (13% to 100%), with a mean (SE) of 69% (4%), while others have estimated a disease-specific mortality rates ranging from 35% to 75% (Gross et al., 2000).

Clifford et al. (2009) used contact and disease transmission models to assess potential impacts of various grazing management strategies on the persistence of several Sierra Nevada bighorn sheep (*O. c. sierrae*) populations. They predicted a 50% probability of catastrophic disease outbreak over a 70-year period if interspecies (domestic and bighorn sheep) contact were reduced to <0.02 contacts per year. Their catastrophic disease outbreak probability estimates were comparable to our findings, which were based on a mean of 1.33 interspecies contacts per year that would result in the likely ($\geq 70\%$) extirpation of all seven herds simulated over the 100-year period. Furthermore, Clifford et al. (2009) assumed that co-habitation was equivalent to contact between bighorn and domestic sheep and that contact would result in disease transmission with either 50% or 100% probability, estimates that were based on reported sheep behavior (Young and Manville, 1960; Onderka et al.,

1988; Foreyt, 1989; Ward et al., 1997; Dubay et al., 2002); previous circumstantial evidence of interspecies contact prior to disease outbreaks (Martin et al., 1996; George et al., 2008); and survivability of the pneumonia pathogen in the environment (Burriel, 1997; Dixon et al., 2002). By contrast, our study allowed the probability of a herd-level outbreak given contact with an allotment to range from 100% to 5%. Nevertheless, even the lowest effective contact probability (5%) resulted in estimated extirpation probabilities ranging from 20% to 53% for the six herds other than the Sheep Mountain herd (which is extirpated with 100% probability under all scenarios).

We relied on expert opinion when estimating the NVN to be 30. Berger (1990) studied extinction rates of 122 bighorn sheep populations in California, Colorado, Nevada, New Mexico and Texas, and estimated that populations of 50 or fewer bighorn sheep would be extinct within 50 years. Singer et al. (2001), based on observations from 41 epizootics, found that bighorn sheep populations with fewer than 50 animals had just a 5% chance of surviving an outbreak; based on these and other results, they concluded that bighorn sheep herds with post-epizootic populations of fewer than 30 individuals would not recover from the outbreak. Singer and Gudorf (1999) found no unequivocal NVN, but suggested a value of 100 individuals if disease is not a factor. If their estimate is closer to reality than the value adopted here, our simulations may have systematically underestimated the proportion of outbreaks leading to herd extirpation across all alternatives.

Results from this analysis were used as inputs by the PNF Forest Supervisor to assess the impact of changes in the allocation of land within the PNF available to domestic sheep. Other considerations, such as socio-economic impact, as well as tribal rights and interests were also considered by decision makers. We believe this modeling approach is useful to USFS managers for assessing the risks and implications of disease transmission between domestic and bighorn sheep.

Conflict of interest statement

No other conflicts of interest exist.

Acknowledgments

This research was funded by the United States Department of Agriculture: Forest Service. We thank the working group convened by the PNF that included bighorn sheep biologists, wildlife disease experts, and representatives from five US National Forests, the Intermountain Regional Office of the US Forest Service, three State fish and wildlife agencies, and four Native American Tribes.

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