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MODELING RISKS OF DISEASE TRANSMISSION FROM DOMESTIC SHEEP TO BIGHORN SHEEP: IMPLICATIONS FOR THE PERSISTENCE AND RESTORATION OF AN ENDANGERED ENDEMIC UNGULATE

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ASSESSING RISK OF DISEASE TRANSMISSION AT THE WILDLIFE-LIVESTOCK

INTERFACE: THE CASE OF THE SIERRA NEVADA BIGHORN SHEEP

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Running head: Disease transmission risk for bighorn sheep

Abstract

Habitat sharing by livestock and wildlife may present a threat to endangered species persistence if diseases affecting domestic animal populations are transmitted to vulnerable wildlife. Respiratory disease transmission from domestic sheep has been implicated in the declines of numerous bighorn sheep populations, but direct evidence is lacking under field conditions. In California, endangered Sierra Nevada bighorn sheep number fewer than 400 individuals. Pathogens present in domestic sheep grazing in public and private areas located within or adjacent to Sierra Nevada bighorn sheep populations may threaten the recovery and persistence of this unique subspecies, but the degree of risk has not been quantitatively evaluated. We used the best available spatial, demographic, and disease data to assess the risk and impact of a respiratory disease outbreak in Sierra Nevada bighorn sheep resulting from contact with domestic sheep. Probabilities of interspecies contact were derived by assessing the spatial overlap of bighorn sheep population kernel utility distributions and public domestic sheep grazing allotments when both species were present on the landscape. Demographic data and modified Reed-Frost disease models were then used to assess the population-level impacts of a respiratory disease outbreak, including herd-level mortality and the possibility of disease spread to adjacent herds of bighorn sheep. Although current management strategies, which included restricting domestic sheep grazing during the bighorn sheep rut, reduced the risk of interspecies contact to less than 2% per year, our model still predicted a 50% probability of at least one respiratory disease outbreak causing $\geq 40\%$ bighorn sheep herd mortality during the next 70 years. Efforts to further minimize or eliminate the potential for interspecies contact include options such as closing allotments within the current distribution of Sierra Nevada bighorn sheep, further restricting grazing during rut, and educating private parties about the disease risk

posed by domestic sheep. These choices will require difficult decisions to balance trade-off costs and benefits to economic livelihoods and natural resource protection.

Introduction

The potential for disease transmission between domestic animals and wildlife presents challenges where livestock are managed in proximity to wildlife populations. Wild ungulates have shared diseases and sometimes served as a reservoir for diseases that cause mortality or undermine the market value of livestock (Caron et al. 2003; Cleaveland et al. 2001; Frohlich et al. 2002). Conversely, disease transmission from domestic animals to wildlife populations has threatened the persistence of many vulnerable wildlife species (Singer et al. 2001; Woodroffe 1999). In many circumstances, managing health threats may require difficult trade-offs between natural resource protection and economic endeavors.

The challenge of balancing species protection and livelihoods is exemplified by the respiratory disease complex affecting North American bighorn sheep. Bighorn sheep are related to domestic sheep (*Ovis aries*) and share many infectious diseases with them, including respiratory diseases of viral and bacterial origin, contagious ecthyma, and psoroptic scabies (Jessup & 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 populations of bighorn sheep (Martin et al. 1996). Experiments and enclosure trials support the hypothesis that bighorn sheep are especially susceptible to pnuemophillic *Manheimia haemolytica* and *Pasteurella* spp. commonly carried by domestic sheep (Callan et al. 1991; Foreyt 1989, 1990, 1994; Onderka & Wishart 1988). Other factors associated with respiratory disease outbreaks in free-ranging bighorn sheep include co-infection

with other pneumophilic bacteria, viruses, or parasites, and environmental stressors (Bunch et al. 1999). Although bighorn sheep that have had no 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 domestic sheep contact (Goodson 1982), the role of domestic sheep in the epidemiology of the bighorn sheep respiratory disease complex remains an important issue (Foreyt 1994).

Sierra Nevada bighorn sheep were listed as endangered by the U.S. Fish and Wildlife Service in 1999; currently about 400 of these unique animals occur in eight small but increasing populations comprising three distinct management units (Fig. 1). The presence of domestic sheep within or adjacent to habitat occupied by Sierra Nevada bighorn sheep may threaten the recovery and persistence of this unique subspecies, but the degree of risk has not been quantitatively evaluated. Although direct contact between Sierra Nevada 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), bighorn sheep have been documented traveling into domestic sheep grazing allotments in recent years, and probability of contact will increase as the Sierra Nevada bighorn sheep numbers increase and the populations expand their geographic range.

Accordingly, we used the best available spatial, demographic, and disease data to assess the risk for and potential impact of a respiratory disease outbreak in Sierra Nevada bighorn sheep resulting from contact between domestic and bighorn sheep. We first evaluated the risk of disease transmission between domestic and Sierra Nevada bighorn sheep 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. Our overall goal

was to identify scientifically-based methods for predicting and reducing risk of contact between the two species and to provide recommendations to those responsible for managing bighorn sheep and the lands they inhabit.

Methods

Study Area

The Sierra Nevada (37°24'N, 118°41'W) extends 650 km along the eastern edge of California, and ranges from 75 to 125 km in width (Hill 2006). The eastern aspect of the range is in a rain shadow and is characterized by desert and steppe ecosystems (Wehausen 1980). Vegetation in the Sierra Nevada varies widely along an elevation gradient; Great Basin sagebrush-bitterbrush scrub is common at low elevations; mid-elevations consist primarily of pinyon-juniper woodland, mountain mahogany, and sub-alpine meadows and forests; and high elevation vegetation consists mostly of sparse alpine meadows (USFWS 2003). Sierra Nevada bighorn sheep utilize a wide range of elevations, from alpine peaks in excess of 4,000 meters to the base of the eastern escarpment as low as 1,450 meters (Wehausen 1980). Bighorn sheep habitat is patchy in the Sierra Nevada, and the population structure of these sheep is one of natural fragmentation (Bleich et al. 1990).

Disease Risk Assessment

We assessed the risk of respiratory disease for three bighorn sheep management units (Northern, Central, and Southern) that differed in their spatial and temporal overlap with domestic sheep. We then focused our analysis on the management unit with the highest risk of disease transmission and evaluated the remaining units in the context of spread of an introduced

disease from that management unit. Data were gathered from demographic monitoring efforts, pertinent literature, and county and government records. We relied on expert opinion if other sources were not available.

Derivation of interspecies contact and disease transmission probabilities

Satellite telemetry (GPS) collar data from 34 (15 male: 19 female) Sierra Nevada bighorn sheep collected by the Sierra Nevada Bighorn Sheep Recovery Program from 2002-2006 were used to determine the utility distribution of the bighorn sheep population in each of the three management units for spring-summer (March-September) and rut (October-November). Utility distributions were calculated using 50%, 60%, 70%, 80%, 90%, and 100% fixed kernel estimators, with a bandwidth of 0.80 (Rodgers & Carr 1998). The fixed kernel estimator was chosen over the adaptive kernel because it has been shown to have lower bias (Fuller et al. 2005). The adaptive kernel method may over-smooth the tails of the distribution resulting in potentially inflated home range estimates (Seaman & Powell 1996). We selected a bandwidth of 0.80 to attenuate measurement/sampling error and to adequately reflect peripheral movement (Powell 2000). Because the kernel represents a sampling of the current bighorn sheep population, we used the 100% volume contour to estimate the variability of ranging behavior for the entire population. A sample of available locations (n=10,215) with a minimum separation of 12 hours between fixes was utilized for kernel estimation to avoid spatial autocorrelation (Swihart & Slade 1985).

Spatial files (Universal Transverse Mercator, North American Datum 1983) containing seasonally grazed domestic sheep allotment boundaries for the year 2005 and 2006 were obtained from the Humboldt-Toyiabe and Inyo National Forests and the Bureau of Land

Management. A layer of spatial data for land ownership within the state of California was constructed to show non-federal land (privately or local government owned) within the study area. The area (km^2) of all federal grazing allotments and non-federal lands located within or adjacent to bighorn sheep habitat was derived from the spatial files or calculated using ArcGIS v9.0 (Environmental Systems Research Institute, Redlands, CA, USA) and Hawth's Tools v3.26 (Beyer 2004).

To account for the potential of stray domestic sheep or herd movements outside an allotment, we created a 1-km buffer around individual allotment boundaries. This distance was based on strays observed at distances of up to 900 m from boundaries and herd movements outside allotments recorded in a sample of radio-collared and observed domestic sheep grazing public lands in the Sierra Nevada in 2005 (California Department of Fish and Game 2006). For each season (spring-summer and rut), the area of overlap of individual buffered grazing allotments within each fixed kernel contour for bighorn sheep populations was calculated.

For each allotment, the probability of interspecies co-habitation, P(IC), was the product of the probability that a bighorn sheep was on the grazing allotment and that a domestic sheep was within one (or more) of the bighorn sheep kernel contours during that season. The probability of a bighorn sheep being within an allotment was defined as the proportion of each kernel contour that overlapped the domestic sheep grazing allotment. Similarly, the probability of domestic sheep being inside bighorn sheep habitat was defined as the proportion of each grazing allotment lying inside bighorn sheep habitat as defined by the kernel contours. Because detailed radiotelemetry data describing the locations of all domestic sheep bands did not exist for every allotment, 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. We then

reduced this spatially-derived probability to account for limited temporal overlap by multiplying the probability of co-habitation for each grazing allotment by the percentage of each season that domestic sheep actually grazed on the allotment (as determined from National Forest Service and Mono County grazing permit records for 2005 and 2006). Data regarding domestic sheep grazing periods was available for only two non-federal land parcels, thus other non-federal parcels were excluded for the P(IC) calculation.

Probabilities of co-habitation for each allotment were summed to yield an overall P(IC) for the spring-summer and rut. These two seasonal probabilities were then combined to determine the total P(IC) for each management unit during a single grazing season. Given the lack of avoidance of domestic sheep by bighorn sheep when they are in proximity, and the interest in and ability of bighorn males to mate with domestic ewes (Young & Manville 1960), we assumed that co-habitation was equivalent to contact between the two species.

The probability of at least one bighorn sheep respiratory disease case was modeled as a product of the total P(IC) and the probability of disease transmission from a domestic sheep to a bighorn sheep. Even though pen transmission studies (Callan et al. 1991; Foreyt 1989, 1990; Onderka & Wishart 1988) indicate that 100% of the bighorn sheep contracted respiratory disease after being co-housed with domestic sheep, detailed transmission data are limited under field conditions. It is likely that some interspecies contacts do not result in transmission of respiratory disease to bighorn sheep. Because we cannot predict which particular contact will result in disease transmission, we modeled the probability of respiratory disease transmission to a bighorn sheep as high (100%), medium (50%), and low (25%). We used the resultant annual probabilities of at least one bighorn sheep respiratory disease case resulting from interspecies contact to investigate the effect of allotment boundary [original (2005) versus restricted (2006)], domestic

sheep stray management [vigilant (no allotment buffer) versus standard (1-km allotment buffer)], and amount of domestic sheep grazing time on the allotments (domestic sheep present throughout season, 2005 grazing schedule, and 2006 grazing schedule).

Model to predict impacts of a respiratory disease outbreak in Sierra Nevada bighorn sheep

We utilized a simple population growth model to predict the bighorn sheep population size. Only females were included in the population growth model as they are the fundamental building blocks for the metapopulation (Bleich et al. 1996) and because the population recovery goals are specified in terms of the number of ewes (USFWS 2003). The discrete logistic population growth equation was used: $N_1 = N_0 + [N_0 * r * (1 - N_0/k)]$, where N_1 = population at time t+1, N_0 = population at time t, r = intrinsic population growth factor (population growth independent of carrying capacity), and k = carrying capacity. Parameters were derived from demographic monitoring and expert opinion, and the model was initiated with female population estimates collected in 2005 by the Sierra Nevada Bighorn Sheep Recovery Program (California Department of Fish and Game, Bishop, CA, USA; Table 1). Beta General distributions were used to account for environmental stochasticity. Lastly, the model parameters were validated by comparing the model predictions to past population growth rates (Wehausen & Stephenson 2005).

To assess potential population-level consequences of a respiratory disease outbreak in bighorn sheep, we created a modified Reed-Frost model (Abbey 1952; Wahlstrom et al. 1998) to predict the cumulative mortality associated with an outbreak. The model was constructed with Microsoft Excel (Microsoft Inc, Redlands, WA) and @Risk software ver. 4.5 (Palisade Corp, Newfield, NY). Parameter estimates were extrapolated from the literature regarding

pasteurellosis in bighorn sheep (Coggins 1988; Coggins & Matthews 1990; Foreyt 1988, 1989) and from expert opinion. A case-time graph estimated from the Lostine bighorn sheep herd *Pasteurella* pneumonia outbreak (Coggins 1988; Coggins & Matthews 1990) was used to fit the model mortality and contact parameters (Table 1). The model was then modified to incorporate three subpopulations in order to reflect the bighorn sheep population structure (USFWS 2003).

A spreadsheet matrix consisting of four disease states: infectious (*C*), persistently infected (*P*), susceptible (*S*), and mortality (*M*) was created, and binomial distributions were used to determine the transition between the disease states, making the initial deterministic model stochastic. In the simulation, infection of bighorn sheep after the incident case could have arisen 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 management unit (k_c). Infected bighorn sheep (State C) could either die (State M) or become persistently infected (State P). 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: $C_{t+1} = S_t * (1-(q_a^{Ct} * q_b^{Pt} * q_c^{C*_t+P*_t}))$, where *t* was the incubation period for the initial infection, 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 was the probability of an individual bighorn sheep avoiding adequate contact with an infected bighorn sheep in the specified time interval, and $P*_t + C*_t$ was the sum of the diseased animals in a neighboring population (Abbey, 1952).

To estimate variability in mortality due to the potential for persistently infected individuals, a second equation was 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. The Solver Add-in for @Risk was used to determine the most appropriate values for m_C, m_P, k_a, and k_b, and r, based on the Lostine 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) an incubation time period (t) of one week for an initial infection; 2) bighorn sheep become infectious to others in the time period following infection ($t+1$); 3) bighorn sheep surviving the first infectious time period ($t+1$) become persistently infected; 4) no fully immune state exists but there is potential for transition back to the susceptible state; 5) random mixing of bighorn sheep within a management unit; and 6) ability of bighorn sheep to travel from one management unit to an adjacent unit within a single time interval.

Finally, the probability of a bighorn sheep respiratory disease 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. Each management scenario simulation was run with 10,000 Monte Carlo iterations and summary statistics were reported for cumulative mortality and time to outbreak.

Sensitivity Analysis

We used the @Risk Advanced Sensitivity Analysis tool to determine which parameters had the most influence on our model. The disease model parameters k_a, k_b, k_c, m_c, m_p, and r were

varied and the resultant mortality proportions for each management unit were evaluated. The k_a parameter 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 3,000 iterations for each of the three outputs.

Results

Probability of interspecies contact and respiratory disease transmission

Bighorn sheep utilized over twice as much area in the Northern and Central management units during rut compared to spring-summer (Table 2), resulting in increased spatial overlap with domestic sheep grazing areas during rut (Figs. 2-3). Bighorn sheep monitored in the South utilized less area during rut, but this finding may be an artifact of small sample size (Table 2). There were no public domestic sheep grazing allotments near the Southern management unit; thus the probability of a disease case in a bighorn sheep resulting from domestic sheep contact could not be determined, and an outbreak starting in the South was not simulated.

The highest probability of a bighorn sheep respiratory disease case resulting from disease transmission from domestic sheep occurred in the North. The likelihood of a case was approximately 7% per year when domestic sheep were allowed to graze the entire season and the 2005 allotment boundaries were used (Table 3). When the actual 2006 grazing schedule and adjusted spatial boundaries were utilized, the annual probability of a bighorn sheep respiratory disease case in the North decreased to 1.2% (Table 3). Most of the reduction in risk was due to the adjusted grazing schedule; adjustment of the spatial boundaries alone resulted in only a small decrease in the probability of a bighorn sheep respiratory disease case.

For comparable management scenarios, the probability of a bighorn sheep respiratory disease case was about 30 times more likely in the Northern than in the Central management unit. Although there is spatial overlap between two allotments near the Central management unit and the bighorn sheep population kernel during rut (Fig. 3b), the current management policy of not grazing sheep in these allotments during rut eliminated the temporal overlap between the species, and resulted in an incalculable probability when actual grazing times were considered. The probability of a bighorn sheep respiratory case was reduced by limiting domestic sheep grazing time (76-81% lower for 2005 and 2006 schedules compared to entire season grazing), by vigilant domestic sheep stray management (48-62% lower if no 1-km spatial buffer), and by reducing the probability of disease transmission (P_d) from a domestic sheep to a bighorn sheep (50% reduction with each decreasing P_d).

Non-federal land that could support domestic sheep was found inside the bighorn sheep fixed kernel contours in all three management units, and similar to above, the amount of non-federal land that overlapped with bighorn sheep population kernels increased during rut for the Northern and Central units (Table 4; Fig 2-3). In the North, 7.0% of the 100% fixed kernel area for rut was occupied by non-federal lands, whereas 1.6% and 1.1% of the 100% fixed kernel area for rut in the Central and South, respectively, were overlapped by non-federal lands. In the Northern and Central units, non-federal lands were present inside all the rut kernel contours, including the core (50%) population kernel (Table 4).

Predicted impacts of a respiratory disease outbreak on Sierra Nevada bighorn sheep populations

Respiratory disease probabilities (P_d) for ten different Sierra Nevada bighorn sheep management scenarios (Table 3) were further evaluated in the epidemiologic simulation model. The predicted cumulative probability of at least one bighorn sheep respiratory disease outbreak causing ≥ 40% herd mortality in the North within the next 70 years varied for the proposed management scenarios. The chance of a significant outbreak was lowest in the North (21%) under the current (2006) grazing strategy, 2006 allotment boundaries, and vigilant stray management (no buffer; model run #8). Probability of a significant outbreak within the next 70 years increased to an almost certainty (98%) in the North when entire season grazing was allowed for 2005 allotment boundaries with relaxed stray management (model run #1;Table 5). Under the current allotment management for the Northern unit (model run #6), the probability of an outbreak causing significant herd mortality was 40% during the next 50 years and increased to 50% when the time period was increased to 70 years. The predicted probability of an outbreak causing significant mortality in the next 70 years in the Central unit was ≤ 14% (Table 5).

The probability of an outbreak spreading and causing appreciable (≥ 4%) mortality in the neighboring population depended upon which unit the outbreak started in. If the outbreak started in the North, the probability of disease spread and resultant appreciable mortality in the Central and Southern units ranged from 4.6 to 9.1% and 0.6 to 1.4%, respectively. Approximately 12% of outbreaks starting in the Central unit spread to, and caused appreciable mortality in, the North and the South.

Model iterations to simulate the spread of a bighorn sheep respiratory disease case resulted in a bimodal distribution of cumulative mortality. In the North, 16% of cases resulted in

0-1% herd mortality while 84% of cases resulted in 15-90% herd mortality (Fig. 4). Approximately 23% of iterations predicted 60% herd mortality. Five percent of cases resulted in outbreaks causing ≥ 72% herd mortality. Overall, herd mortality from 33-76% was predicted most frequently (Fig. 4). Ninety-three percent of respiratory disease cases originating in the North resulted in ≤ 4% herd mortality in the Central unit (Fig. 5). The remaining 7% of cases from the North spread to and resulted in 44-75% herd mortality in the Central unit, with approximately 5% of these cases resulting in ≥ 59% herd mortality (Fig. 5). Approximately 99% of respiratory disease cases originating in the North resulted in ≤ 4% herd mortality in the Southern unit (Fig. 6). The remaining 1% of cases from the North spread to and resulted in 50-66% herd mortality in the South.

Seventeen percent of cases originating in the Central unit caused 0-1% herd mortality, while 83% of cases resulted in 40-81% mortality. Herd mortality from 45-77% was predicted for 69% of cases. Eighty-eight percent of respiratory disease cases originating in the Central unit resulted in ≤ 4% herd mortality in the Southern unit. The remaining 12% of cases from the Central unit spread to and resulted in 40-71% herd mortality in the South. Eighty-eight percent of respiratory disease cases originating in the Central unit resulted in ≤ 4% herd mortality in the Northern unit. The remaining 12% of cases from the Central unit spread to and resulted in 36-80% herd mortality in the North.

The average predicted time to the first respiratory disease case in the Central and Southern units for an outbreak that started in the North was 24.2 weeks (SD=19.58, Range: 2 – 121 weeks) and 49.7 weeks (SD=28.69, Range: 14 – 130 weeks), respectively. In comparison, the average predicted time to the first respiratory disease case in the Northern and Southern units

for an outbreak that started in the Central unit was 24.2 weeks (SD=19.58, Range: 2 – 121 weeks) and 24.7 weeks (SD=19.26, Range: 2 – 145 weeks), respectively.

Model Sensitivity Analysis

Mortality proportion in the North was sensitive to changes in the number of adequate contacts with cases within the same management unit (k_a) and the probability of recovery from the persistently infected state (r). Mortality proportion showed the largest change as k_a increased from one (10.0% mortality) to two contacts (51.0% mortality). Mortality proportion was resistant to changes in *r* from values of 0.25 (46.6% mortality) to 0.75 (50.8% mortality), but as *r* decreased from 0.25 toward 0 the mortality proportion increased to 71.2%. 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 unit and 57.6% in the South when $k_c = 0.25$.

Discussion

Limitations of our analysis

Data substantiating direct transmission of respiratory pathogens between domestic and bighorn sheep in a free-ranging situation are lacking, due largely to the inherent logistical difficulties in obtaining such data (Martin et al. 1996). Accordingly, some of our model parameters rely on transmission data from trials conducted in an enclosure or experimental situation. Additionally, habitat characteristics that may influence the probability of interspecies

contact were not explicitly accounted for in our model but have been addressed by others

(Johnson et al. 2006). Location data from a sample of bighorn sheep that wore GPS collars were

used to construct the fixed kernels and provides a conservative estimate of the range currently

utilized. Additional aerial survey, VHF-collar, and opportunistic observational data show that

Sierra bighorn sheep have been observed outside our GPS-based population kernels (see

Appendix). Furthermore, we did not attempt to model future movements significantly beyond the

current distribution of bighorn sheep that may occur as a result of population growth or

exploration by rams seeking mates. Therefore, we consider our estimates of interspecies co-

habitation to be conservative. Finally, 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 variation in the ability

of herders to prevent contact when in proximity to bighorn sheep; are not quantifiable and thus,

could not be modeled.

Findings, recommendations, and priorities for future research

Our risk assessment supports the premise that current (2006) measures designed to reduce

interspecies contact and disease transmission have lowered the annual probability of respiratory

disease in Sierra Nevada bighorn sheep. However, despite current efforts, there still remains a

50% chance that a bighorn sheep respiratory outbreak causing significant herd-level mortality

will occur in the next 70 years. This risk is due largely to the presence of multiple domestic

sheep grazing allotments within currently utilized Sierra Nevada bighorn sheep habitat in the

Northern management unit and that domestic sheep are grazed in some of those allotments

during rut when our data indicate bighorn sheep expand their range. The high risk of contact in

the North is supported by habitat suitability analyses showing that preferred bighorn sheep spring-summer range habitat overlaps parts of four domestic sheep allotments (Johnson et al. 2006) and by data indicating a northward expansion of bighorn sheep (Wehausen & Stephenson 2004). In comparison, the current temporary closure of the two allotments closest to bighorn sheep in the Central management unit has reduced the risk of interspecies contact below detection limits used in our analysis. If these allotments were re-opened and grazed, our model predicts up to a 14% chance of a significant bighorn sheep respiratory disease outbreak in the Central unit in the next 70 years. Although the risk of disease is lower in the Central than in the North, an outbreak starting in the Central management unit has a higher probability of spreading to adjacent populations.

If elimination of the risk of interspecies contact (thereby eliminating the probability of respiratory disease transmission to bighorn sheep from domestic sheep) is a recovery goal, a precautionary approach (deFur & Kaszuba 2002) is needed. At a minimum, domestic sheep grazing should not occur within the known population utility distribution of Sierra Nevada bighorn sheep. Given that seasonal changes in this distribution occur, it may be possible to graze some allotments during the spring-summer as long as vigilant herd management is practiced to reduce strays and respond to wandering bighorn sheep, and domestic sheep are removed well before the onset of rut.

Our model also predicts that it may take over two years for a respiratory disease outbreak starting in the North to spread throughout the larger metapopulation. This time lag is supported by data from previous outbreaks in bighorn sheep (Goodson 1982) and suggests that persistently infected individuals are significant for retaining and perpetuating disease among susceptible bighorn sheep. The persistently infected state is likely a factor in bighorn sheep populations that

show apparent "self-starting" outbreaks of respiratory disease when no clinical signs have been reported for many weeks. Practically, this suggests that active surveillance of at risk populations of bighorn sheep may be necessary for long periods of time after a respiratory disease outbreak has occurred in an adjacent population.

Additional research focused on bighorn sheep movements and habitat utilization in the Sierra Nevada is needed. 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 & Bleich 2005). Further, more detailed data showing where domestic sheep graze on existing allotments are needed to better estimate the probability of interspecies contact in this system. One method of obtaining more detailed domestic sheep movement data would be to provide herders handheld GPS units so that all herd movements can be recorded and updated in real-time. Such an approach would also save labor for those agencies responsible for managing risk, and could contribute valuable information for range management purposes.

Additional information regarding the risk of contact with domestic sheep held on private allotments and personal property is also needed, as these areas occur adjacent to a substantial part of the Sierra Nevada occupied by bighorn sheep. These areas represent potential for year-round risk, as "hobby sheep" may be present at any time and owners may be less aware than land managers about the potential for disease transmission to nearby bighorn sheep. Reduction of this risk could be achieved by presenting education programs to community groups and private allotment owners and, perhaps, by providing incentives for people not to maintain domestic sheep in areas close to bighorn sheep habitat.

Conservation Implications

Although respiratory disease outbreaks may occur infrequently in Sierra Nevada bighorn sheep populations as a result of domestic sheep contact, the population-level impacts of one outbreak are significant in terms of predicted mortality and the potential to spread to an adjacent population and possibly throughout the entire range. Their currently small population size may put Sierra bighorn sheep at high risk of extinction if a respiratory disease outbreak occurs. Previous research has shown that only 5% of herds with less than 50 bighorn sheep persisted after a pneumonia epidemic (Singer et al. 2000). Furthermore, our model includes only three-subpopulations with low connectivity between the management units. As these isolated populations grow, increased movement of bighorn sheep between these populations will enhance the risk of a respiratory disease outbreak propagating throughout the metapopulation. In order for healthy metapopulations to function there must be genetic exchange between populations (Bleich et al. 1996). Unfortunately, this benefit may come at the expense of increased potential for disease spread unless risk is mitigated. Given this trade-off, movements by Sierra Nevada bighorn sheep must continue to be monitored. Further, it is expected that the populations will continue to expand naturally and artificially due to legally-mandated recovery efforts (USFWS 2003).

To reduce the risk of disease transmission between domestic and bighorn sheep, many wildlife managers advocate maintaining a zone of no contact between the species (Gross et al. 2000; Martin et al. 1996; Schommer & Woolever 2001). Policies to maintain separation between the two species have been adopted by wildlife departments and land management agencies (BLM 1992, 1998; Schommer & Woolever 2001), and separation of domestic sheep from bighorn sheep ranges by $\geq$ 23 km has been recommended (Singer et al. 2000; Singer et al. 2001).

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 (SNBSRP 2004). The propensity for contact is exacerbated further by bighorn sheep males that are attracted to female domestic sheep (Young & Manville 1960). We used a conservative 1 km buffer zone for reducing contact. This very small zone could only be safely maintained via thorough monitoring of both bighorn sheep and domestic sheep. Appropriate separation distances are difficult to determine because male bighorn sheep have moved up to 75 km (Berger 2004), and male Sierra Nevada bighorn sheep have traveled distances of up to 53 km (T. Stephenson, unpublished).

When natural resources are managed for both domestic animals and wildlife, conflicts inevitably arise. The management recommendations based on our data are quite conservative from a wildlife conservation perspective, but are intended to serve as a starting point for land use decisions involving a diverse group of stakeholders working to achieve consensus-based management solutions to the incompatibility of domestic and bighorn sheep. By employing an integrated demographic and disease modeling approach based on the best available data, we have provided a quantitative tool useful for assessing the risk of interspecies disease transmission, and for evaluating the relative risks associated with various land management strategies.

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

Description of variables	Notation	Value, distribution or formula	Source
Infectious disease model			
mean # of contacts adequate to transmit disease made by an infected bighorn in a single time period	k_a	2	Coggins 1988; Solver add-in using Lostine outbreak data
probability of adequate contact between a susceptible bighorn and a persistently infected bighorn	k_b	0.02 (1 contact/year)	T. Stephenson, unpublished
probability of adequate contact with an infected bighorn in an adjacent management unit	k_c	0.0002 (1 contact/10 years)	Sierra bighorn location data; T. Stephenson, unpublished
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 (recovery in 20 weeks)	Foreyt 1990
incubation period (time period) for the initial infection	t	1 week	
Population growth model			
# ewes in the Northern management unit	N_n	16	Wehausen 2005
# ewes in the Central management unit	N_c	40	Wehausen 2005
# ewes in the Southern management unit	N_s	92	Wehausen 2005
Probability of a case in at least one bighorn	Pcase	variable	Spatio-temporal overlap data
Carrying capacity of Northern management unit	K_n	RiskBetaGeneral (2,2,40,100) Mean=70, SD=13.42	Wehausen, pers. comm. T. Stephenson, unpublished
Carrying capacity of Central management unit	K_c	RiskBetaGeneral (2,2,50,125) Mean=88, SD=16.77	Wehausen pers. comm T. Stephenson, unpublished
Carrying capacity of Southern management unit	K_s	RiskBetaGeneral (2,2,155,410) Mean=283, SD=57.02	Wehausen, pers. comm. T. Stephenson, unpublished
Average ewe lifespan	L	12 years	V.Bleich, unpublished
Ewe recruitment rate Northern management unit	B_n	RiskBetaGeneral (12,67,0,1) Mean=0.15, SD=0.04	Modeled from Sierra bighorn monitoring data 2002-2005 (CDFG, unpublished)
Ewe recruitment rate Central management unit	B_c	RiskBetaGeneral (45,140,0,1) Mean=0.24, SD=0.03	Modeled from Sierra bighorn monitoring data 2002-2005 (CDFG, unpublished)
Ewe recruitment rate	B_s	RiskBetaGeneral (70,177,0,1) Mean=0.28, SD=0.03	Modeled from Sierra bighorn monitoring data 2002-2005 (CDFG, unpublished)
Ewe mortality rate (all recovery units)	M	RiskBetaGeneral (2,22,0,1) Mean=0.08, SD=0.05	Modeled from average ewe lifespan (L)

Table 2. Fixed kernel distribution estimates of the area (km^2) utilized by GPS-collared Sierra

Nevada Bighorn Sheep during the spring-summer (March-September) and rut (October-

November).

	Area (km^2) utilized by monitored Sierra Nevada Bighorn Sheep					
	Management Unit					
	Northern		Central		Southern*	
Probability that bighorn range is captured	Summer	Rut	Summer	Rut	Summer	Rut
50%	10.9	32.8	8.3	19.6	29.5	11.2
60%	16.6	43.0	10.9	27.2	39.2	15.4
70%	24.4	54.4	14.3	36.8	51.9	20.5
80%	36.3	74.2	19.3	49.1	70.2	27.3
90%	54.2	101.6	28.3	68.2	102.3	37.1
100%	359.9	737.5	181.6	432.7	501.5	208.0

* Location data only available both seasons for the Sawmill/Mt. Baxter herd

Table 3. Respiratory disease probabilities for ten different Sierra Nevada bighorn sheep management scenarios. Probabilities of a case of respiratory disease were derived from spatio-temporal overlap data for bighorn and domestic sheep. Varying management strategies included: domestic sheep grazing schedule [sheep present entire season or actual grazing schedule (< entire season)], grazing allotment spatial boundaries [original (2005) vs. restricted (2006)], and with or without a 1-km spatial buffer to account for short distance domestic sheep straying.

Disease Model Run	Bighorn Management Unit	Domestic sheep grazing schedule	Grazing allotment spatial boundary	1-km Management Buffer	Annual probability of bighorn respiratory disease case
1	*Northern*	Entire season	2005	Yes	0.077
2	*Northern*	Entire season	2006	Yes	0.067
3	*Northern*	Entire season	2005	No	0.033
4	*Northern*	Entire season	2006	No	0.027
5	*Northern*	Actual 2005	2005	Yes	0.015
6	*Northern*	Actual 2006	2006	Yes	0.012
7	*Northern*	Actual 2005	2005	No	0.008
8	*Northern*	Actual 2006	2006	No	0.005
9	*Central**	Entire season	2006	Yes	0.003
10	*Central**	Entire season	2006	No	0.001

* Annual probability of a bighorn respiratory disease case was not calculable when actual grazing schedule used

Table 4. Area of overlap (in km^2) between Sierra Nevada bighorn sheep population fixed kernel distribution contours for three management units (Northern, Central, and Southern) during the spring-summer (March-September) and rut (October-November), and non-federal land that could support domestic sheep.

| Probability that bighorn range is captured | Management Unit | | | | | |
| | Northern | | Central | | Southern* | |
	Summer	Rut	Summer	Rut	Summer	Rut*
100%	15.19	52.93	3.00	7.09	4.45	2.42
90%	1.47	2.88	1.06	2.10	0	0
80%	1.25	1.58	0.34	2.04	0	0
70%	0.33	0.31	0.00	1.88	0	0
60%	0.00	0.18	0.00	1.35	0	0
50% (core)	0.00	0.01	0.00	0.44	0	0

* Kernel data only available both seasons for the Sawmill/Mt. Baxter herd

Table 5. Predicted cumulative probability of at least one respiratory disease outbreak in Sierra Nevada bighorn sheep causing ≥ 40% herd mortality. Ten model runs (detailed in Table 3) representing different management regimes were evaluated.

Management Unit	Model Run	Time (years)				
		≤ 5	≤ 10	≤ 25	≤ 50	< 70
Northern	1	26.02	45.27	77.84	95.09	98.44
Northern	2	24.14	42.45	74.87	93.69	97.79
Northern	3	12.35	23.17	49.25	74.22	83.77
Northern	4	10.19	19.34	41.57	65.86	77.31
Northern	5	5.75	11.18	25.64	44.71	55.86
Northern	**6***	**4.95**	**9.65**	**22.41**	**39.80**	**50.36**
Northern	7	3.10	6.09	14.55	26.97	35.20
Northern	8	1.71	3.40	8.28	15.88	21.23
Central	9	1.08	2.14	5.27	10.26	13.88
Central	10	0.39	0.78	1.94	3.85	5.27

* Current management regime for allotments near the North
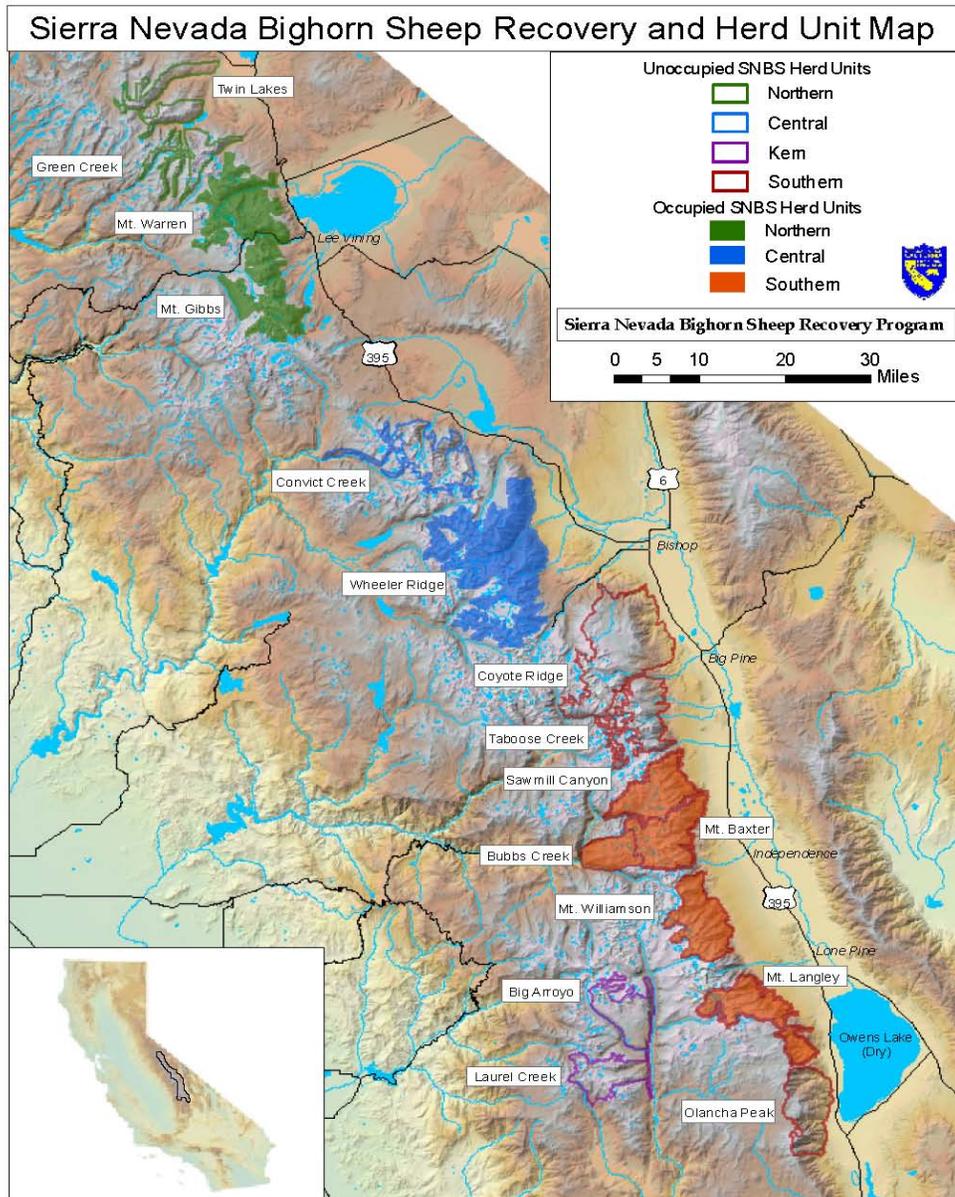
Figure 1. Map of Sierra Nevada Bighorn Sheep (SNBS) range in California, USA showing the
Northern, Central, and Southern management units currently occupied by bighorn sheep (solid
colors) and additional management units currently unoccupied by bighorn sheep (open colors).
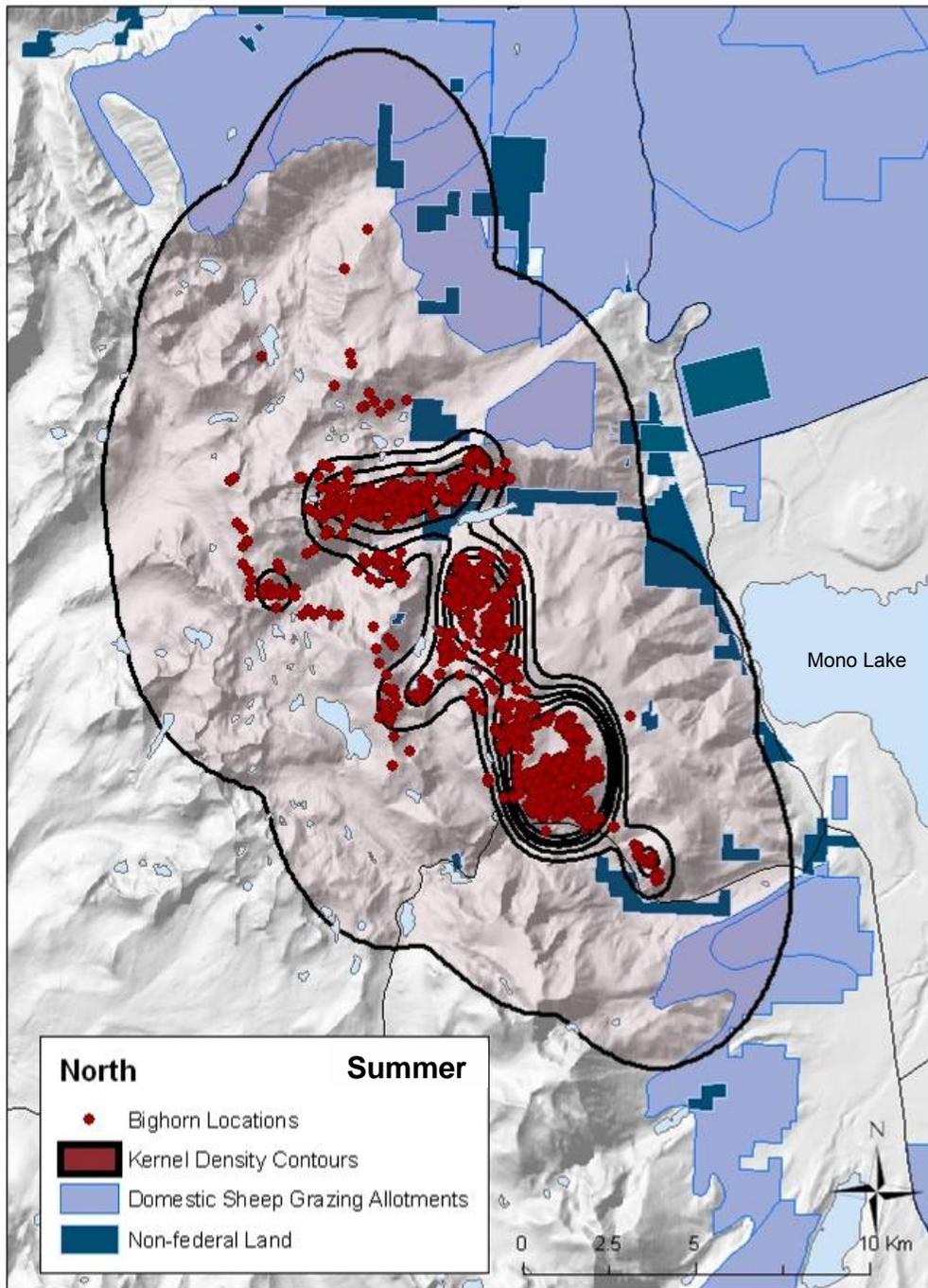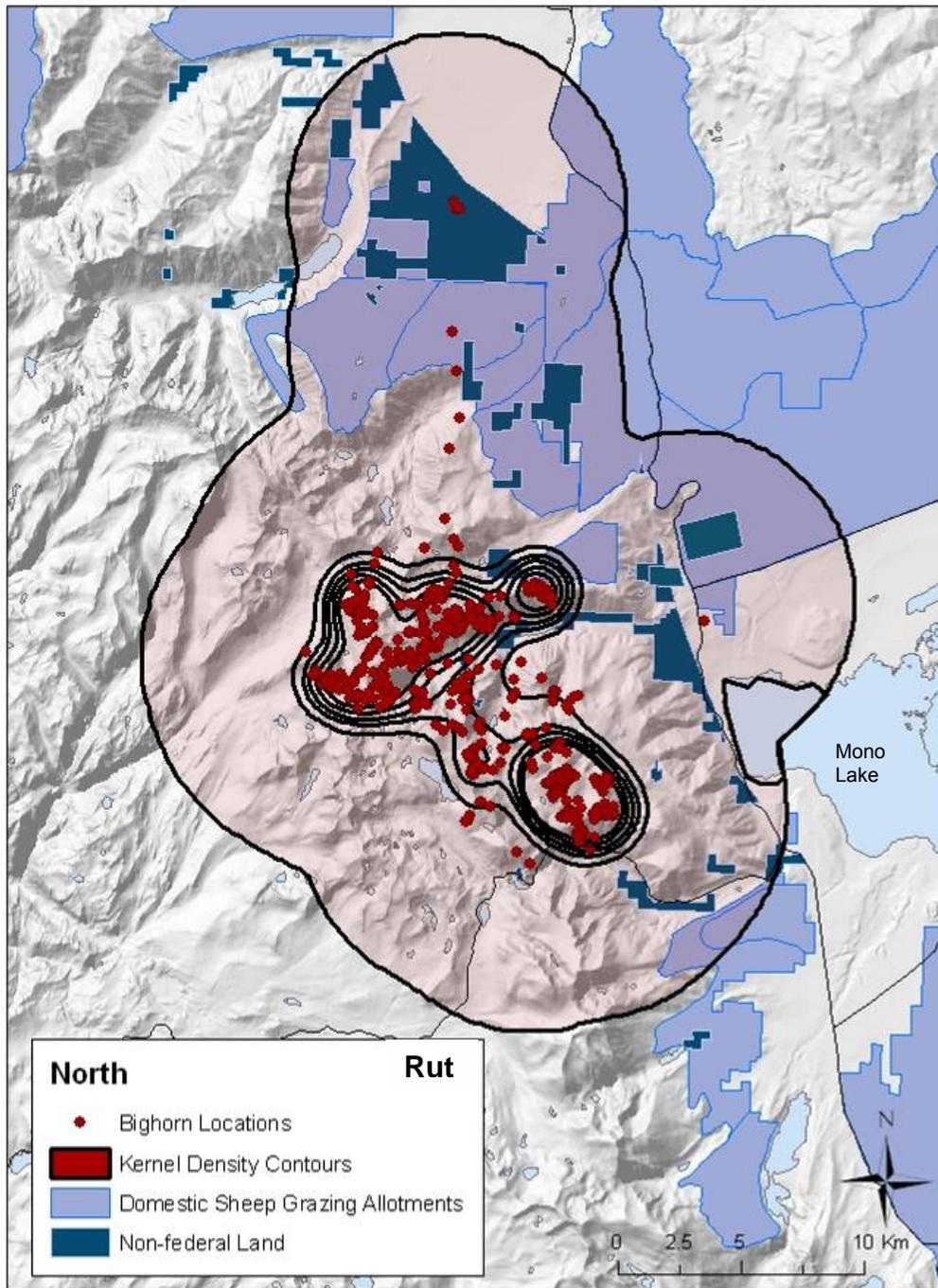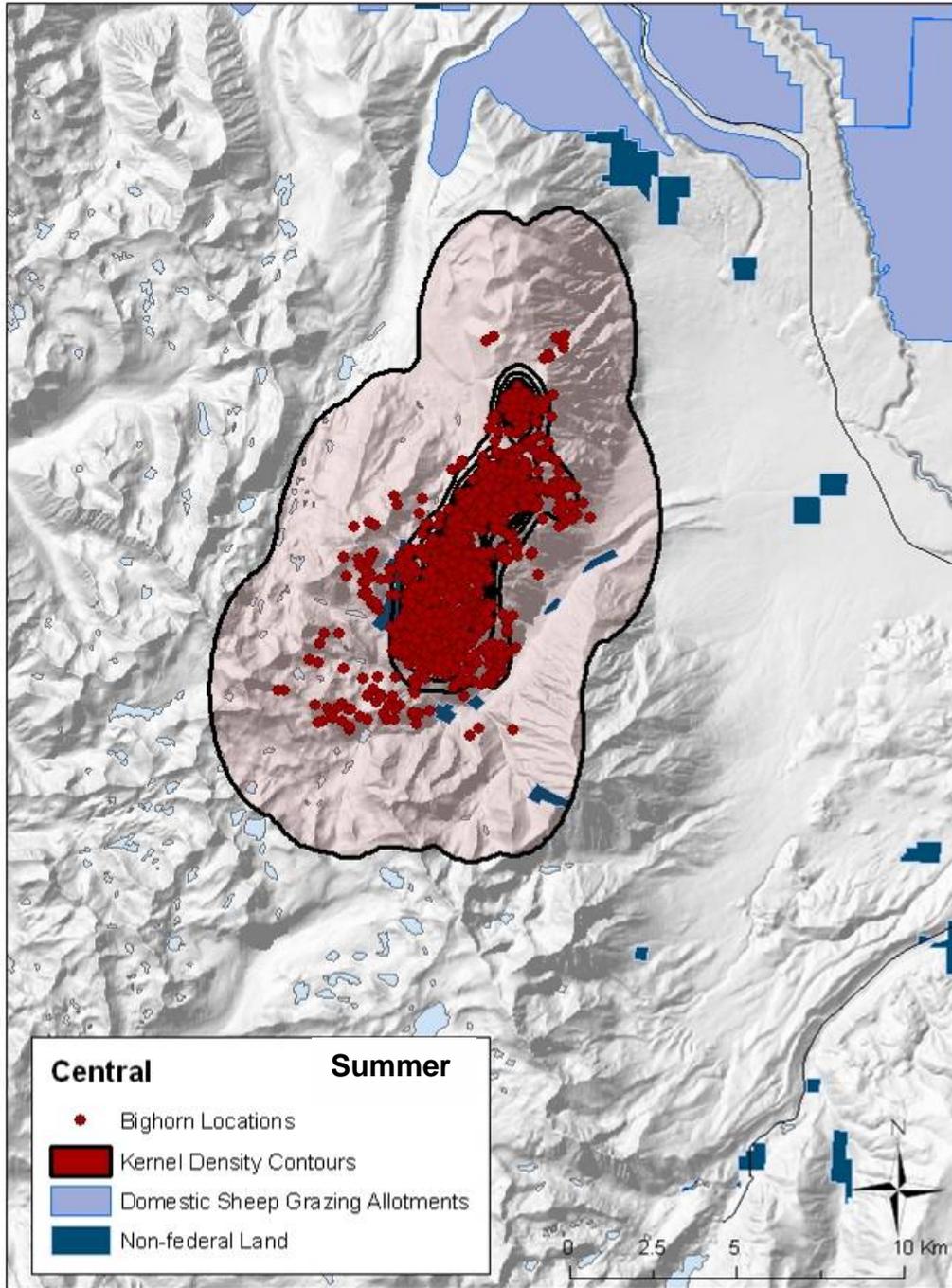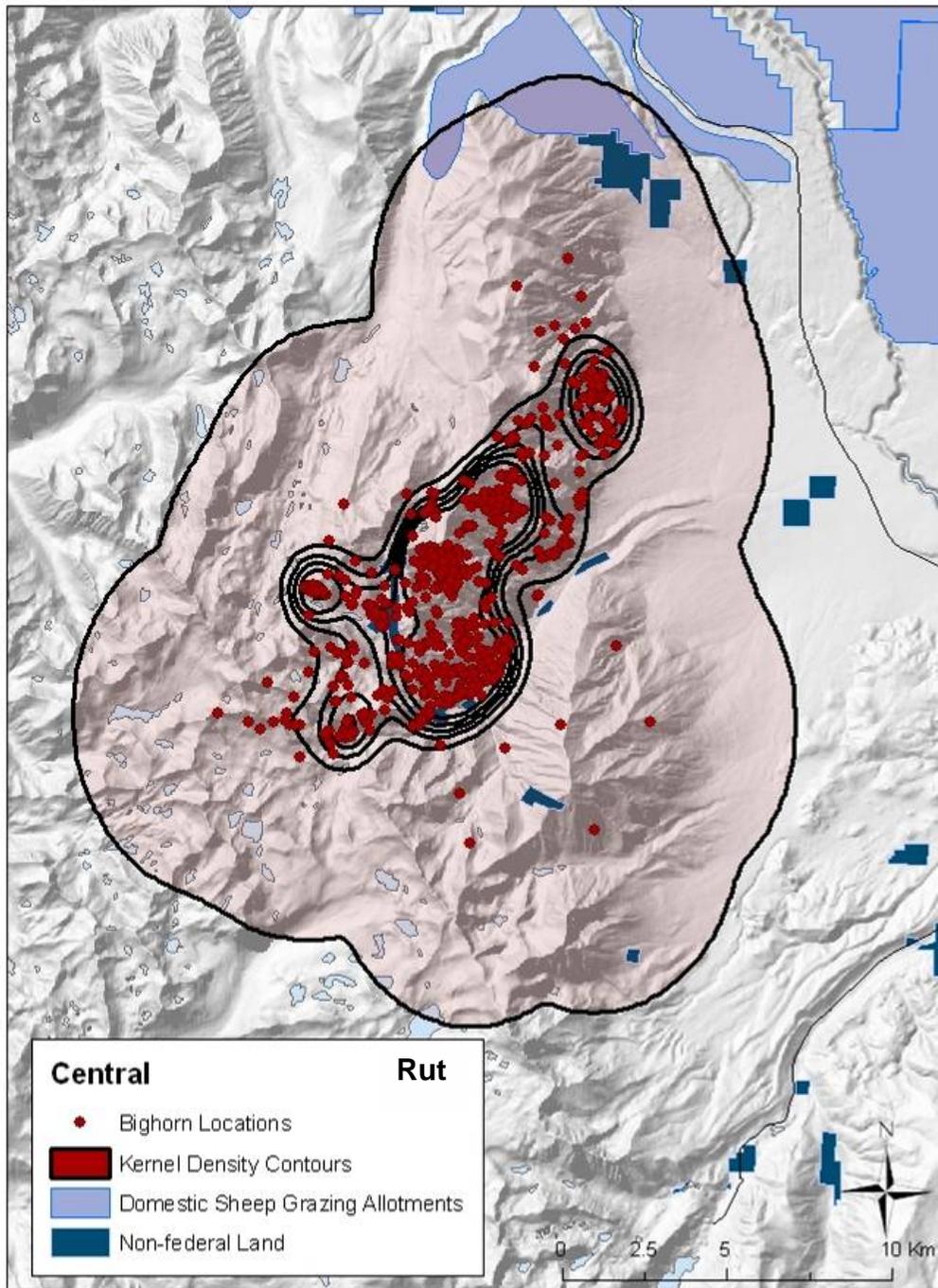
Figure 2a. Map demonstrating extent of spatial overlap between federal domestic sheep allotments, non-federal lands, and the 50% (core), 60%, 70%, 80%, 90%, and 100% (outer contour) fixed kernel distributions for GPS-collared bighorn sheep in the Northern management unit during the spring-summer (March-September).

Figure 2b. Map demonstrating extent of 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 bighorn sheep in the Northern management

unit during rut (October-November).

Figure 3a. Map demonstrating extent of 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 bighorn sheep in the Central management unit during the spring-summer (March-September).

Figure 3b. Map demonstrating extent of 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 bighorn sheep in the Central management unit during rut (October-November).
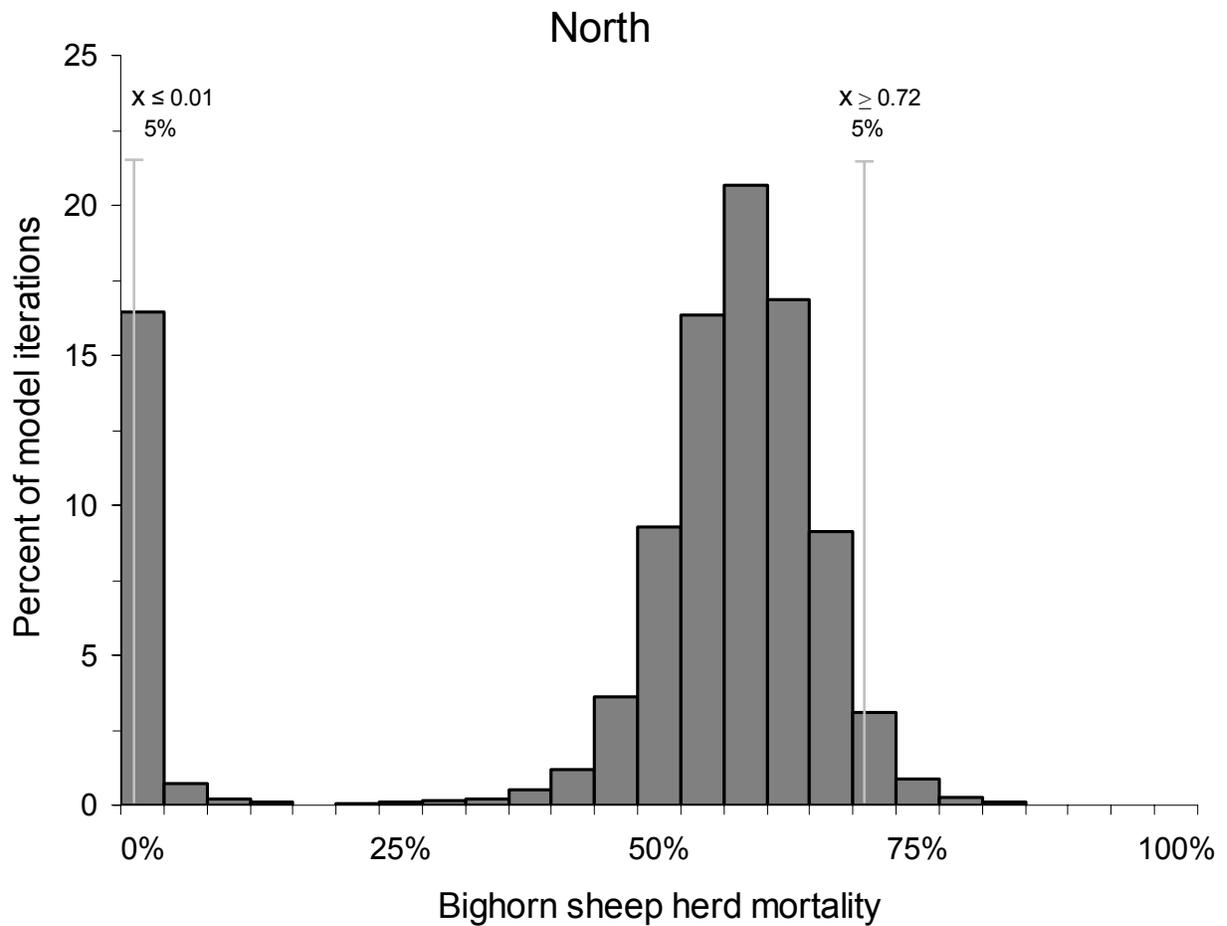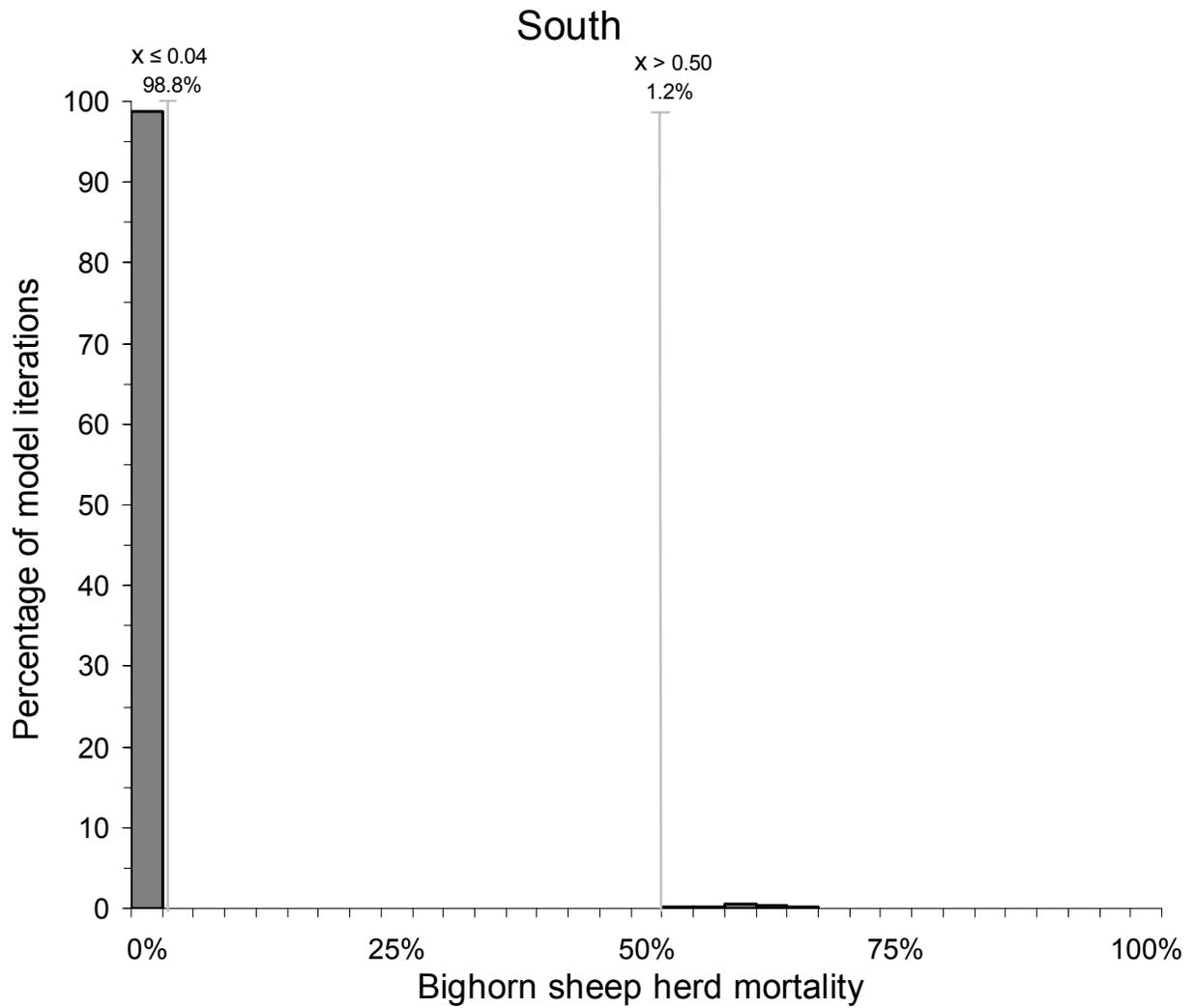
Figure 4. Frequency distribution (based on percent of 10,000 model iterations) of Sierra Nevada bighorn sheep herd mortality in the Northern management unit resulting from a bighorn sheep respiratory disease case starting within the unit.
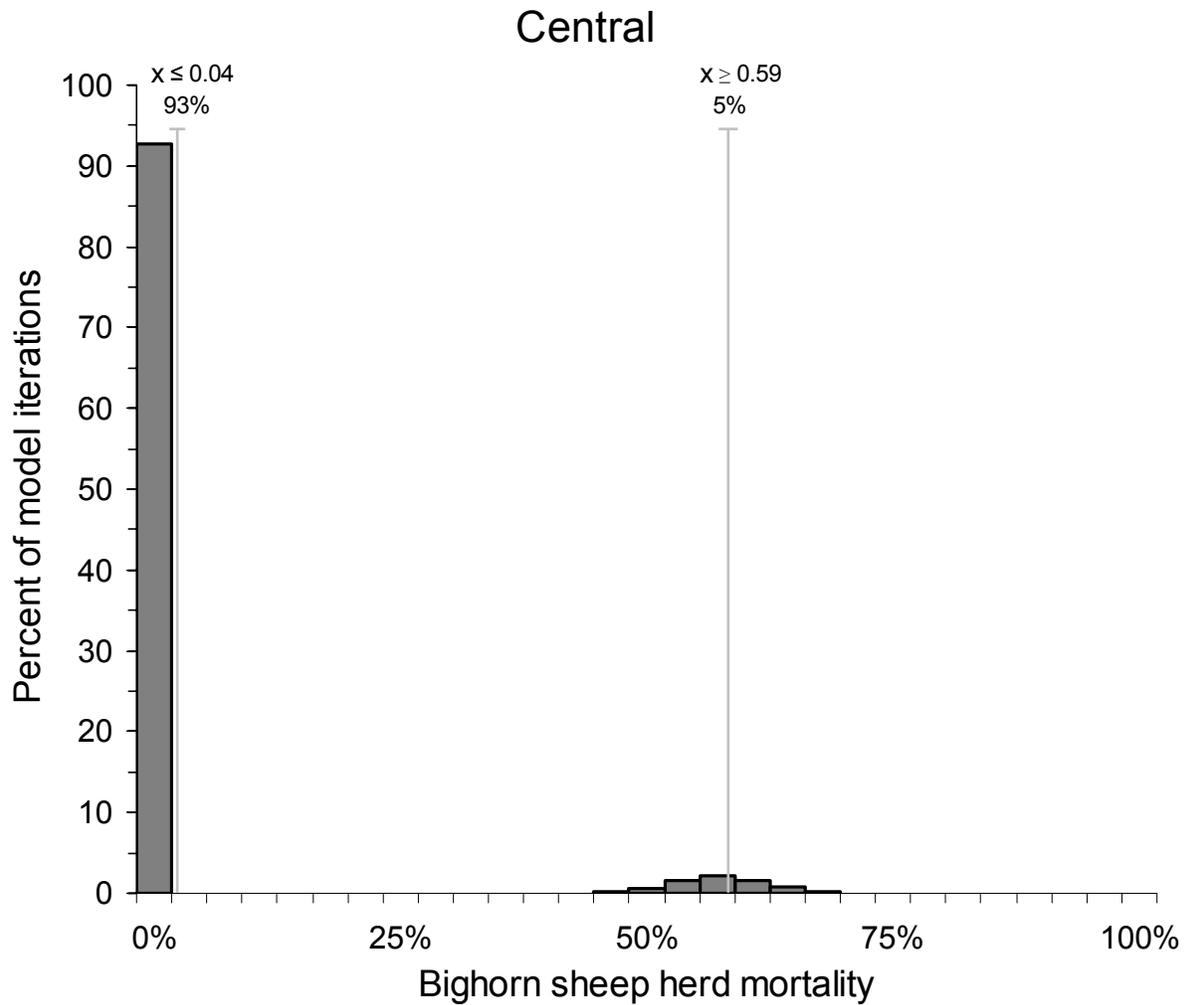
Central

Figure 5. Frequency distribution (based on percent of 10,000 model iterations) of Sierra Nevada bighorn sheep herd mortality in the Central management unit resulting from a bighorn sheep respiratory disease case that originated within the Northern management unit.

Figure 6. Frequency distribution (based on percent of 10,000 model iterations) of Sierra Nevada bighorn sheep herd mortality in the Southern management unit resulting from a bighorn sheep respiratory disease case that originated within the Northern management unit.

Appendix. Revised kernel contours that incorporate VHF telemetry locations

The risk analysis was conducted using location data acquired only from GPS collars. GPS collars acquire multiple locations per day for each animal that wears one; hence, they provide a thorough assessment of all areas used by those animals. The decision was made to limit risk modeling to those animals wearing GPS collars because initial interest focused on clearly defining travel paths of wandering bighorn sheep and because GPS collar data has minimal sampling bias.

In 2006, additional monitoring of eight (5 male: 3 female) Sierra Nevada bighorn sheep in the Northern management unit and 13 (7 male: 6 female) Sierra Nevada bighorn sheep in the Central management unit was conducted using VHF radiotelemetry and visual observations. Although the level of detail provided by VHF collars is not as great as GPS collars, there have been considerable data acquired through the use of conventional telemetry by ground searches and by aircraft. The additional information provided by VHF data have further defined movements of the population throughout the Sierra Nevada.

The additional maps provided in this appendix illustrate a larger area of concern for disease risk than was presented in the main report because additional observation data were incorporated. Bighorn that wore VHF collars in the Central and Northern management units illustrate to a more complete extent the movements of bighorn sheep in the Sierra Nevada. The kernel polygons presented in this appendix are larger than those in the report because of the additional animals included and their respective locations. The increased overlap between bighorn kernels and domestic allotments indicated by the inclusion of these additional data would further increase probabilities of contact and the risk of disease transmission.

Figure A1 includes the locations of a male that traveled from the Mt. Warren Herd Unit (Northern management unit) south to Laurel Mountain; consequently, the kernel contours represent an increase in risk of interspecies contact between the Northern and Central management units during summer because of the overlap of allotments. The kernel contours for the Northern management unit during rut did not change substantially with the addition of VHF data (Fig. A2). Additional locations from the Central management unit during spring-summer expanded the kernel contours a bit to the north, but domestic allotments remained outside of the kernels (Fig. A3). Most importantly, northerly movements by rams from Wheeler Ridge (Central management unit) resulted in kernel contours that overlap a number of units of an allotment (Rock Creek) during rut (Fig. A4).

When combined, GPS and VHF collared animals in 2006 accounted for approximately 32% (39/121) of the estimated bighorn sheep population in the Northern and Central management units. Although our sampling effort is extensive, we cannot evaluate the movements of the remaining 68% of bighorn sheep that are not collared. The additional VHF collar data presented in this Appendix show that GPS sampling efforts alone underestimated the full extent of areas used by bighorn; further emphasizing the need for continued monitoring of this population using multiple modalities and the need to take a precautionary approach when assessing disease risk in wildlife populations.
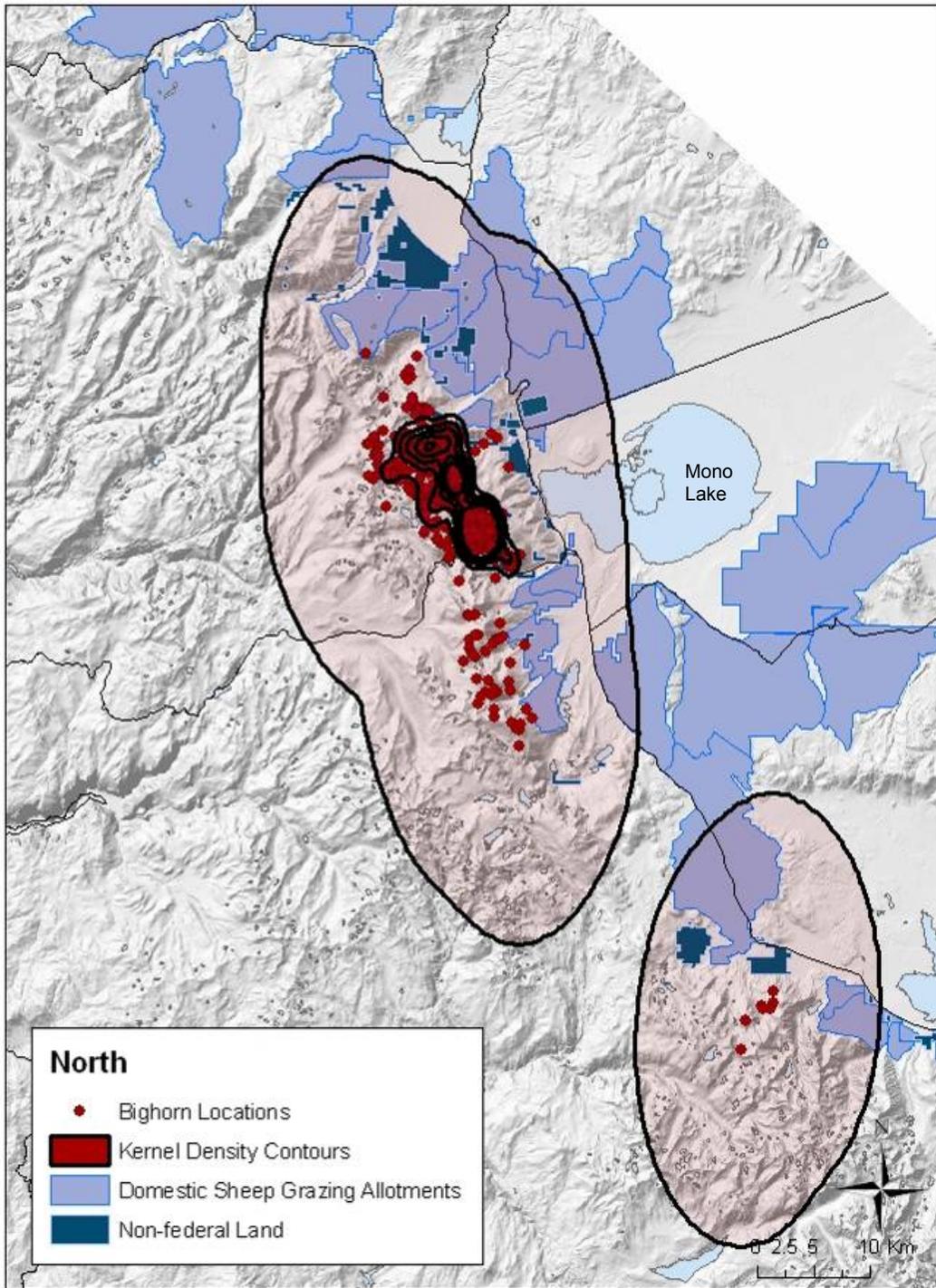
Figure A1. Sierra Nevada bighorn sheep locations and kernel contours incorporating additional

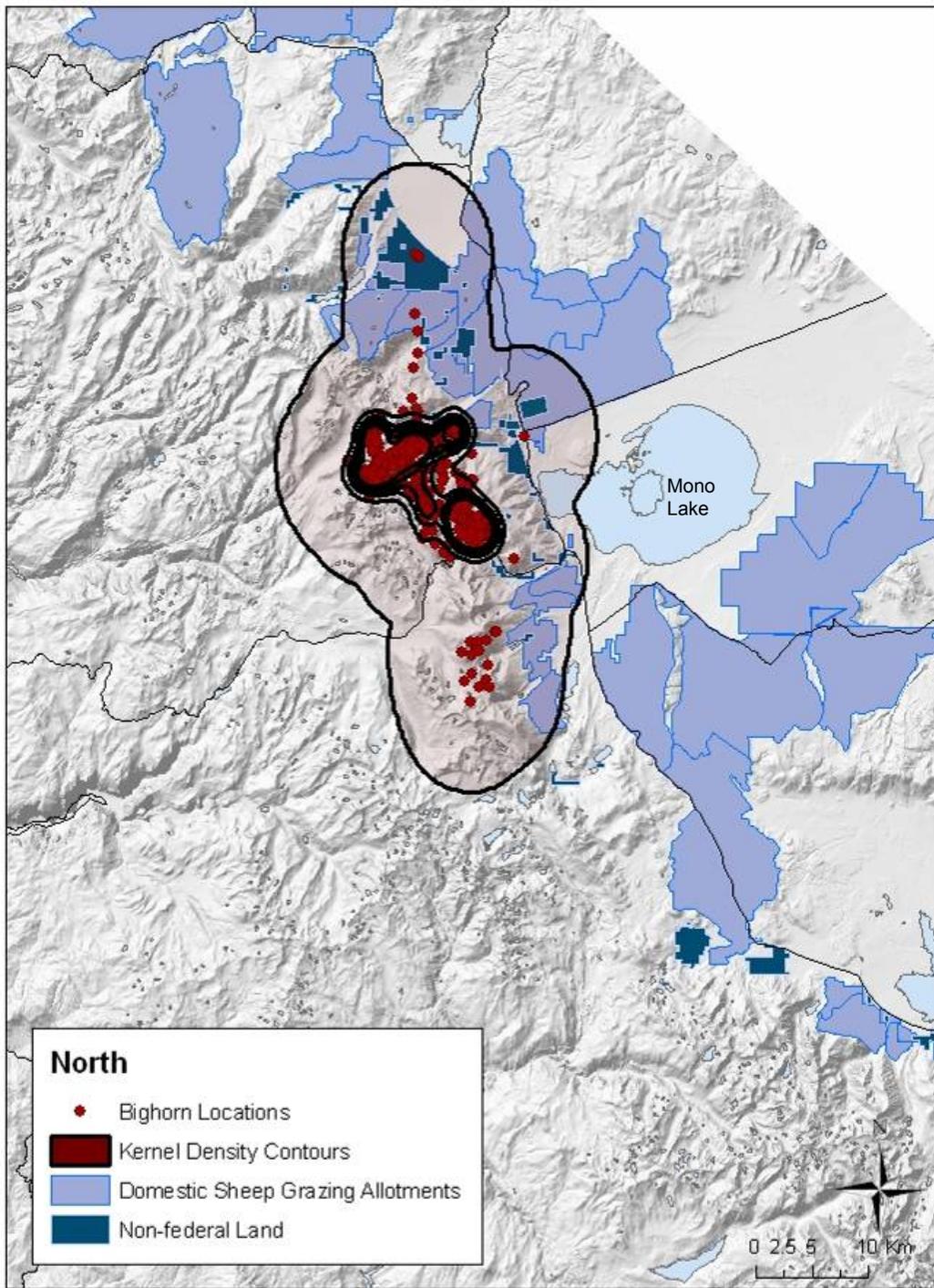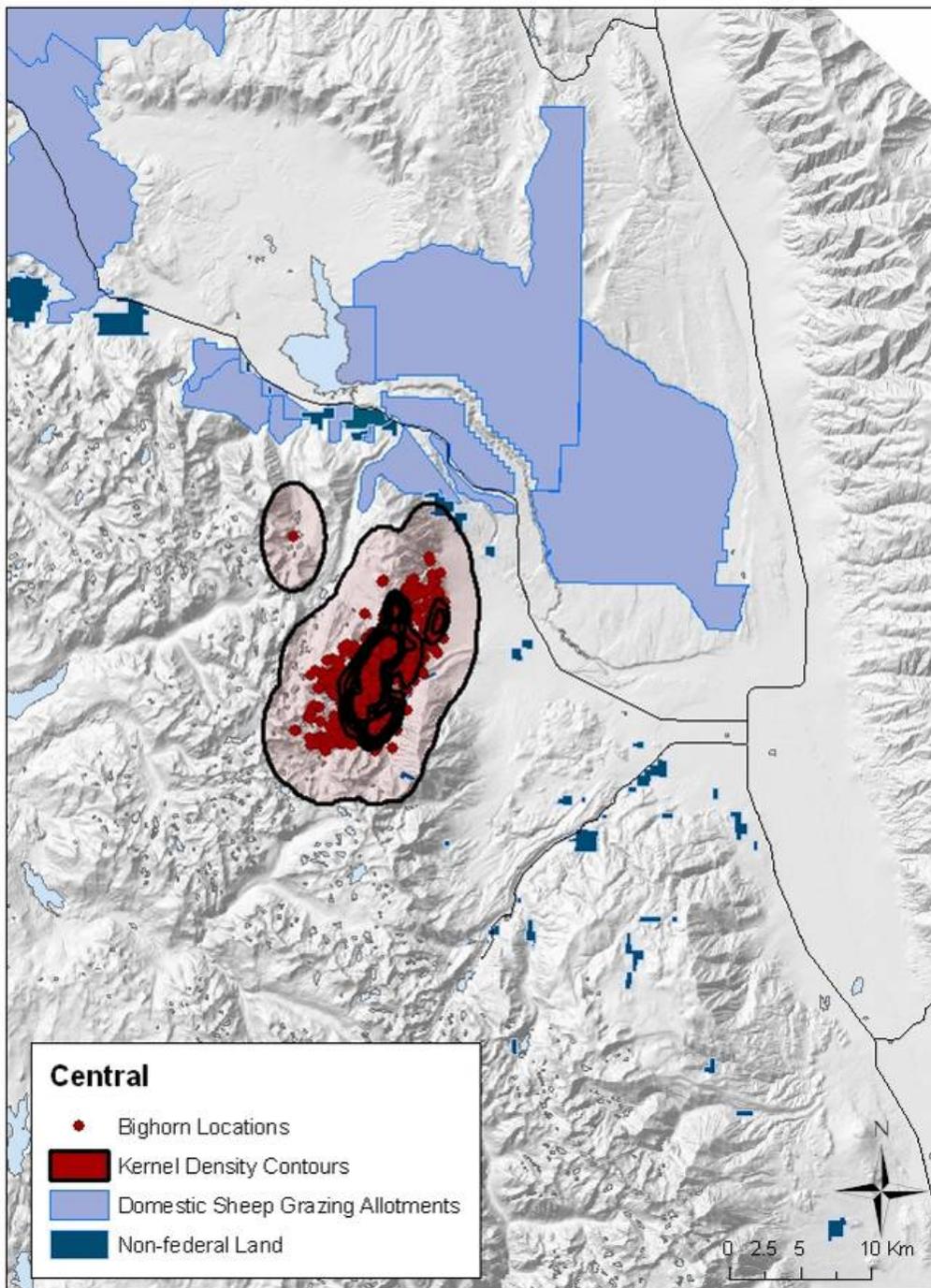data from VHF-collared bighorn sheep in the Northern management unit during spring-summer.

Figure A2. Sierra Nevada bighorn sheep locations and kernel contours incorporating additional data from VHF-collared bighorn sheep in the Northern management unit during rut.

Figure A3. Sierra Nevada bighorn sheep locations and kernel contours incorporating additional data from VHF-collared bighorn sheep in the Central management unit during spring-summer.
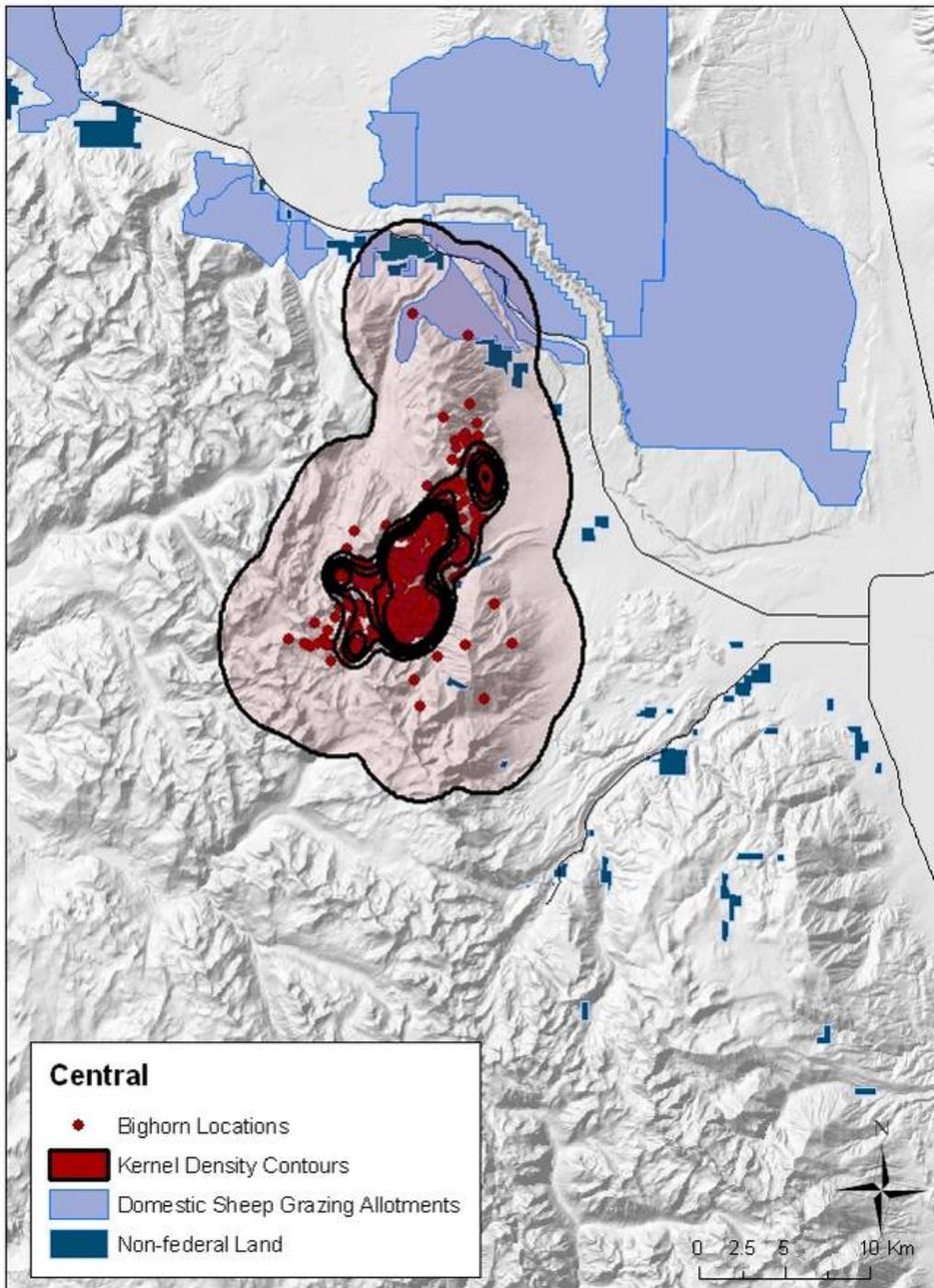
Figure A4. Sierra Nevada bighorn sheep locations and kernel contours incorporating additional

data from VHF-collared bighorn sheep in the Central management unit during rut.