Research Article

Behavioral Connectivity Among Bighorn Sheep Suggests Potential for Disease Spread

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ABSTRACT Connectivity is important for population persistence and can reduce the potential for inbreeding depression. Connectivity between populations can also facilitate disease transmission; respiratory diseases are one of the most important factors affecting populations of bighorn sheep (*Ovis canadensis*). The mechanisms of connectivity in populations of bighorn sheep likely have implications for spread of disease, but the behaviors leading to connectivity between bighorn sheep groups are not well understood. From 2007–2012, we radio-collared and monitored 56 bighorn sheep in the Salmon River canyon in central Idaho. We used cluster analysis to define social groups of bighorn sheep and then estimated connectivity between these groups using a multi-state mark-recapture model. Social groups of bighorn sheep were spatially segregated and linearly distributed along the Salmon River canyon. Monthly probabilities of movement between adjacent male and female groups ranged from 0.08 (±0.004 SE) to 0.76 (±0.068) for males and 0.05 (±0.132) to 0.24 (±0.034) for females. Movements of males were extensive and probabilities of movement were considerably higher during the rut. Probabilities of movement for females were typically smaller than those of males and did not change seasonally. Whereas adjacent groups of bighorn sheep along the Salmon River canyon were well connected, connectivity between groups north and south of the Salmon River was limited. The novel application of a multi-state model to a population of bighorn sheep allowed us to estimate the probability of movement between adjacent social groups and approximate the level of connectivity across the population. Our results suggest high movement rates of males during the rut are the most likely to result in transmission of pathogens among both male and female groups. Potential for disease spread among female groups was smaller but non-trivial. Land managers can plan grazing of domestic sheep for spring and summer months when males are relatively inactive. Removal or quarantine of social groups may reduce probability of disease transmission in populations of bighorn sheep consisting of linearly distributed social groups. © 2016 The Wildlife Society.

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Understanding population connectivity and the spatio-temporal dynamics of animal populations are fundamental issues in population ecology. Connectivity influences the probability of population persistence (Brown and Kodric-Brown 1977, Noss 1987, Runge et al. 2006, Mills 2007, Lowe and Allendorf 2010) and reduces the potential for inbreeding depression (Brown and Kodric-Brown 1977,

Mills and Allendorf 1996, Mills 2007, Lowe and Allendorf 2010). Connectivity can also influence the transmission of disease through a spatially structured population (Noss 1987; Simberloff and Cox 1987; Hess 1994, 1996; Crooks and Sanjayan 2006; Mills 2007). The way in which disease spreads through a population is often a result of how individuals in that population come into contact (Barbour and Mollison 1990). The number and extent of these contacts may be determined by factors affecting social organization such as group size, density, composition, dispersal rates, and mating systems (Altizer et al. 2003).

Diseases, specifically respiratory diseases, are one of the most important factors affecting populations of bighorn

sheep (*Ovis canadensis*) over the last several decades (Foreyt and Jessup 1982, George et al. 2008). Contact with domestic sheep (*O. aries*) can introduce pathogens that result in respiratory disease and fatal pneumonia in bighorn sheep (Foreyt and Jessup 1982, George et al. 2008, Besser et al. 2012), but after initial exposure pathogens are likely maintained in the population and spread by bighorn sheep (Cassirer et al. 2013). Connectivity potentially influences the spread of pneumonia outbreaks within a bighorn population. Cassirer and Sinclair (2007) hypothesized that seasonal behavior patterns may be a cause of increased pneumonia mortality during fall and early winter. George et al. (2008) hypothesized that increased contact between individuals during the rut could explain timing of pneumonia epidemics, whether they resulted from endemic or introduced pathogens. Sells et al. (2015) reported that Euclidean distance between 43 herds of bighorn sheep in Montana did not predict pneumonia epizootics over 34 years, but the presence of neighboring herds with a current or historical epizootic within a 14.5-km buffer was highly predictive.

Like many ungulates, bighorn sheep form spatially structured, sexually segregated groups and remain in these groups during the majority of the year (Geist 1971, Festa-Bianchet 1991, Ruckstuhl 1998). Male groups consist primarily of adult males (Festa-Bianchet 1991), whereas female groups include a mix of adult females and lambs, yearlings, and subadults of both sexes (Festa-Bianchet 1991, Ruckstuhl 1998). These groups of individuals that interact often and share part of a common home range throughout most of the year—hereafter referred to as social groups—are considered the most basic demographic and genetic units of bighorn populations (Geist 1971, Rubin et al. 1998, Boyce et al. 1999). Population connectivity for bighorn sheep is thus based on the movement of individuals among and between these groups.

Movement of males, particularly during the rut, is generally thought to connect populations of bighorn sheep, (Geist 1971, Bleich et al. 1997, Boyce et al. 1997, Rubin et al. 1998), but the timing and extent of this movement is variable. In Montana, DeCesare and Pletscher (2006) observed several long distance summer movements (up to 33 km) by males in one herd that connected them to other herds of bighorn sheep. In Alberta, researchers reported differing seasonal dispersion patterns in males and documented movements up to 48 km (Festa-Bianchet 1986*a*). Schroeder et al. (2010) reported that mean daily movements of males were greater than those of females.

Interactions between females of different social groups may also be an important component in connectivity, although these interactions are highly variable. In non-continuous habitats like those in the Peninsular ranges in California, researchers found that groups of females correspond to distinct mountain ranges and females rarely cross patches of unsuitable areas to interact with other social groups of females (Rubin et al. 1998, Boyce et al. 1999). Similarly, DeCesare and Pletscher (2006) did not observe any movements of females that overlapped other social groups

of females in Montana. In contrast, Festa-Bianchet (1986*b*, 1991) demonstrated that female social groups in Alberta commonly intermingled with members of other groups of females.

We evaluated connectivity of bighorn sheep living along the Salmon River in Idaho, USA, where social groups were distributed linearly along the river (Mack and Robinson 2009, Mack 2011). The bighorn sheep population along the Salmon River is thought to include 2 subpopulations comprising groups inhabiting the Salmon River canyon (~188 sheep) and the South Fork Salmon River canyon (~124 sheep; Mack and Robinson 2009). The population is unique because it has never been extirpated and is considered one of the only native bighorn sheep herds in Idaho (Idaho Department of Fish and Game [IDFG] 2010). Nonetheless, disease-related mortalities were observed in this subpopulation as early as the late 1870s and were primarily attributed to scabies introduced by domestic sheep (Buechner 1960). During the early 1990s, herds across the Salmon River subpopulation experienced all-age die-offs (believed to be disease related) that reduced numbers by approximately 50% (IDFG 2010).

We designed our research to determine the degree of seasonal interaction between and within social groups of male and female bighorn sheep to better understand connectivity within the lower Salmon River canyon. We hypothesized that connectivity within the population was primarily due to male movements, which would be highest during the rut, and movement of females between social groups was less than that of males because of strong philopatry and limited dispersal. Alternatively, we hypothesized that connectivity within the population was due to both male and female movements between social groups, regardless of sex, because bighorn sheep are gregarious, females form nursery groups in the summer, and groups in our study area were connected by bighorn sheep habitat.

We used multi-state models to estimate probabilities of individual bighorn sheep transitioning between areas occupied by different male and female social groups. This approach has been used to model transition probabilities between wintering areas of Canada geese (*Branta canadensis*; Hestbeck et al. 1991), breeding colonies of roseate terns (*Sterna dougallii*; Spendelow et al. 1995), and navigation of dams by Chinook salmon (*Oncorhynchus tshawytscha*; Buchanan and Skalski 2010). We assumed that transition probabilities between social groups of bighorn sheep estimated by the models were an index of the probability of sheep within one group contacting those in another (i.e., connectivity based on individual movements).

STUDY AREA

Our study area was in west-central Idaho and included the lower portion of the Little Salmon River drainage, the Salmon River canyon upstream from Riggins, Idaho to Big Mallard creek, the lower part of the South Fork Salmon River, and upper portions of the Payette River drainage. Landscapes were rugged and mountainous and elevations ranged from 245 m in river canyons to 2,695 m in the Salmon River Mountains.

Lower elevation areas were dominated by bunchgrass associations (bluebunch wheatgrass [*Pseudoroegneria spicata*] and Idaho fescue [*Festuca idahoensis*]), deciduous shrubs in riparian areas, and upland shrub communities. Douglas fir (*Pseudotsuga menzeisii*) and ponderosa pine (*Pinus ponderosa*) were found in riparian stringers and north slopes with forested habitats becoming dominant in upper elevations. The majority of the study area was publicly owned, consisting largely of United States Forest Service, Bureau of Land Management, and state of Idaho lands. Average annual precipitation ranged from 42.7 cm to 65.9 cm. Annual temperatures ranged from $-4.2°C$ to $33.6°C$.

METHODS

Capture and Monitoring

We captured bighorn sheep from November 2007 to January 2013 by using helicopters to net-gun, dart, or herd animals into a drive net, or darting them from a jet boat. We fitted bighorn sheep with either a global positioning system (GPS) store-on-board (ATS G2110; Advanced Telemetry Systems, Isanti, MN, USA), GPS satellite (North Star Science and Technology, King George, VA, USA), or very high frequency (VHF) radio-collar (ATS M2500; Advanced Telemetry Systems, Isanti, MN, USA or Lotek LMRT-4; Lotek Wireless Inc., Newmarket, Ontario, Canada). Males marked with GPS collars were also fitted with a VHF collar. Capture and handling was performed by IDFG or contracted personnel and was approved by the University of Montana's Institutional Animal Care and Use Committee (AUP 012-11). The GPS collars were programmed to collect 1–4 locations per day. Additionally, all collared animals were located by Nez Perce Tribe (NPT) biologists every 2 weeks using fixed-wing aircraft except for May–July and September–October when flights were performed weekly.

We combined radio-location data for each radio-collared animal from 2007–2012. We excluded all animals with <20 locations from the analysis (Mack and Robinson 2009). Based on previous work on the population that found no radio-marked bighorn sheep moved >4.8 km from the Salmon or South Fork Salmon rivers (Mack and Robinson 2009), we considered locations occurring >5 km from the river as outliers and omitted them from analyses.

Determination of Social Groups

We delineated social groups of bighorn sheep through hierarchical clustering of individual home range overlap. We estimated individual home ranges for each radio-collared bighorn sheep as 95% utilization distributions (UDs) generated by a fixed kernel estimator (Worton 1989; R package adehabitatHR, Calenge 2006). We chose the smoothing factor based on the optimum value for the reference bandwidth (href; Worton 1989) because it most accurately estimates linear home ranges (Blundell et al. 2001) such as those in our population. Our VHF relocation error was estimated to be <400 m (C. Mack, Nez Perce Tribe, unpublished data) so we set the grid size to 400 m. We estimated overlap between each pair of UDs using volume of intersection of UDs (VI; Seidel 1992, Millspaugh et al. 2004), which ranges from 0 (no overlap) to 1 (complete overlap).

To identify distinct social groups, we performed agglomerative hierarchical cluster analysis (R package pvclust; Suzuki and Shimodaira 2006) using VI for each possible pairing of UDs. This analysis depicts groupings of individuals with high VI as separate clades in a dendrogram (Suzuki and Shimodaira 2006). We ran clustering analyses separately for males and females using the average linking method (Bethke et al. 1996) with 1,000 bootstrap replications each to determine the number of groups of males and females in our study area. We used the multiscale bootstrap procedure in the pvclust package to estimate P-values (Shimodaira 2004, Suzuki and Shimodaira 2006). We used an alpha of 0.01 to be conservative with respect to group designations. We plotted the social group UDs in a geographic information system (GIS) using ArcMap 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA).

To define geographical states for our multi-state models, we combined locations of all animals within each social group (identified by cluster analysis) and generated monthly 95% UDs for each group (Home Range Tools; Rodgers et al. 2007) using 20% of href to best capture the highly linear areas occupied by social groups (Anderson and Dickson 2012). We also estimated UDs for each social group in ArcGIS to allow visual examination by month to determine the period when movements of bighorn sheep within each group were the most restricted (i.e., UDs were smallest). We determined that UDs were smallest in July, August, and September; we therefore combined locations of all animals in each social group during this time period and estimated 95% UDs (with 20% href); we used these UDs to define the geographic states in our model. We defined boundaries between these groups based on gaps between the 95% isopleths of the UDs. In the case of overlapping 95% isopleths of the UDs, we divided the area of overlap and the locations within it evenly between the 2 groups. In all cases locations within the area of overlap were <10. We then performed clustering analysis on a combined dataset of all males and females for the months of July, August, and September to determine if any male or female social group UDs overlapped in space and warranted combination into a single geographic state.

Connectivity

We built a daily encounter history for each individual from 8 November 2007–5 January 2013 where we assigned each location for each sheep to a single geographical state on each day. Encounter histories also included a binary covariate for sex to test its effect on the probability of transition. In addition, we modeled the effect of the rut (15 Oct–15 Jan) and the effect of the lambing period (15 Apr–30 Jun) on the probability of transition. We also tested the effect of more general summer (May–Sep) and winter (Oct–Apr) seasons on the probability of transition (Anderson and Dickson 2012).

We used maximum likelihood to optimize a spatial, multistate, mark-recapture model (Devnieau et al. 2010, 2014) in

program R, allowing us to estimate the probability that a bighorn sheep from one state (i.e., social group) on a given day would transition into another on the following day. We modeled transition probabilities in a stepping-stone fashion where animals must transition between neighboring states first (i.e., to move from state A to state C, the individual must to go through state B), where the transition probability is $\Psi_{AC} = \Psi_{AB} \times \Psi_{BC}$. We also constrained the model to incorporate the most efficient movement process (i.e., when calculating movement from B to C, if the animal moved from state B to A, back to B, and then to C, we did not include the B to A movement in the calculation of the B to C transition probability).

We generated 16 models including all combinations of sex, rut, lambing season, winter, and summer. We also tested for interaction between these variables by including all combinations of interactions between seasons and the other covariates. We ranked these models using Akaike's Information Criterion (AIC; Akaike 1974). We considered models with ΔAIC < 2 to be well supported by the data (Burnham and Anderson 1998). We calculated variances using the delta method in R package emdbook (Bolker 2016). We used 2-sample t-tests to compare average monthly transition probabilities between summer and winter seasons within and between each sex.

RESULTS

Determination of Social Groups
We collared 30 females (18 VHF and 12 GPS; Table 1) and 26 males (8 VHF and 18 GPS), 17 and 21 of whose collars were active, respectively, over multiple years yielding 25,077 locations. Agglomerative hierarchical cluster analysis indicated there were 8 adjacent social groups arranged linearly within the Salmon River canyon. The females-only cluster analysis resulted in 4 groups, which we named the Wind River, Indian Creek, Jersey Creek, and South Fork female groups. The males-only cluster analysis also resulted in 4 groups and designated the Manning Bridge, Bull Creek, Blowout Creek, and South Fork male groups. The combined (Jul–Sep) cluster analysis supported 6 geographic group designations (Fig. 1). These were similar to the group designations above but combined the Blowout Creek males and the Jersey Creek females, and also combined the South Fork male and female groups. The Indian Creek females did

not cluster entirely together in the same clade in the combined analysis but, based on the sex-specific cluster analysis and ground observations (Mack 2011), we designated them as a group. For our multi-state analyses, we therefore used the following states: Manning Bridge male group (state MR), Wind River female group (state WE), Bull Creek male group (state BR), Indian Creek female group (state IE), Jersey Creek female group and Blowout Creek male group (state JB), and South Fork female group and South Fork male group (state SF; Fig. 2).

We estimated a total of 10 transition probabilities (Ψij) between the 6 geographic states (Fig. 2). The model of probability of transition that included summer season ($\beta = 0.28$), winter season ($\beta = 0.23$), sex ($\beta = 0.74$), and interactions between summer and sex ($\beta = 0.31$), and winter and sex ($\beta = 0.72$), was best supported by the data (Table 2), receiving 86% of the AIC weight. Standard errors for all beta estimates were < 0.001.

Connectivity
We found evidence of connectivity among groups for both sexes with males generally having higher probabilities of transition than females. Monthly transition probabilities along the Salmon River canyon (states MR through JB) ranged from 0.08 (± 0.004) to 0.76 (± 0.068) for males and 0.05 (± 0.132) to 0.24 (± 0.034) for females (Table 3). Connectivity between the Salmon River canyon and the South Fork (states JB and SF), however, was comparatively restricted. Monthly transition probabilities between the Jersey-Blowout and the South Fork groups ranged from 0.003 (± 0.000) to 0.046 (± 0.032) for males and 0.002 (± 0.001) to 0.009 (± 0.003) for females (Table 3).

Mean probability of any male making any transition during the winter (0.41 ± 0.022 SE) was higher ($t_{11} = -0.34$, $P < 0.01$) than during the summer (0.12 ± 0.015). Mean probability of any female making any transition did not differ ($t_{15} = 0.74$, $P = 0.47$) between summer (0.09 ± 0.014) and winter (0.07 ± 0.011). Mean probability of making any transition during the summer did not differ ($t_{15} = 0.61$, $P = 0.55$) between males (0.13 ± 0.010) and females (0.10 ± 0.008). Mean probability of making any transition during the winter was higher for males (0.39 ± 0.028; $t_{15} = 3.70$, $P < 0.01$) than for females (0.08 ± 0.006).

DISCUSSION

Connectivity among social groups of bighorn sheep in the Salmon River region of Idaho was due primarily to movements of males among social groups and not females, consistent with findings of other research (Bleich et al. 1997, Boyce et al. 1997, Rubin et al. 1998, DeCesare and Pletscher 2006, Schroeder et al. 2010). We found that mean monthly probabilities of transition between social groups for males were nearly 5 times greater than those for females in winter, but not in summer. Mean monthly transition probabilities for females did not vary seasonally, whereas those for males were nearly 3.5 times higher in winter during the rut than in summer. We did not detect the same degree of movements by males outside of the rut as reported by DeCesare and

Table 1. Number of bighorn sheep fitted with radio-collars in 8 social groups in the Salmon River drainage, west central Idaho, USA from 2008–2012.

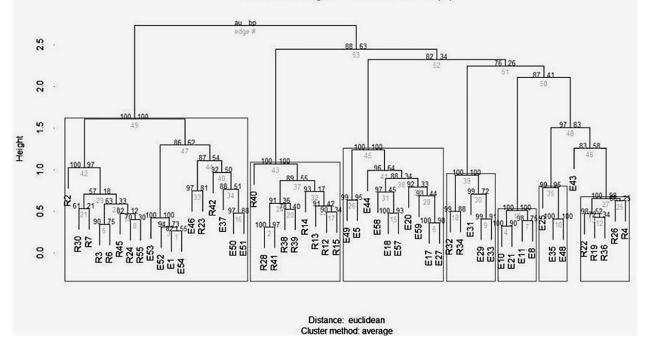| Social group	2008 M	2008 F	2009 M	2009 F	2010 M	2010 F	2011 M	2011 F	2012 M	2012 F
Bull	1		4		5		4		2	
Indian		3		4		6		6		5
Jersey-Blowout	4	1	5	1	6	2	6	2	6	7
Manning	4		5		8		8		4	
South Fork			2	3	2	3	2	3	1	2
Wind River		1		5		6		6		7
Total	9	5	16	13	21	17	20	17	13	21

Figure 1. Dendrogram from agglomerative hierarchical clustering analysis of radio-collared bighorn sheep in the Salmon River drainage in west central Idaho, USA, during July–September 2007–2013. Boxes delineate social groups with 99% confidence. AU = approximately unbiased *P*-value, BP = bootstrap probability, edge # = number of shortest paths containing a given edge, and height = relative proximity of clusters.

Pletscher (2006); probabilities of transition for males were much lower during the summer months.

Probabilities of transition between groups of bighorn sheep were highly variable in the Salmon River canyon. Individuals in groups near the center of bighorn sheep distribution generally had higher transition probabilities than those in groups near the edges. Not surprisingly, transition probabilities for adjacent female groups such as Indian Creek and Jersey Creek were 3 times higher than those of female groups separated by a male group (e.g., Wind River and Indian
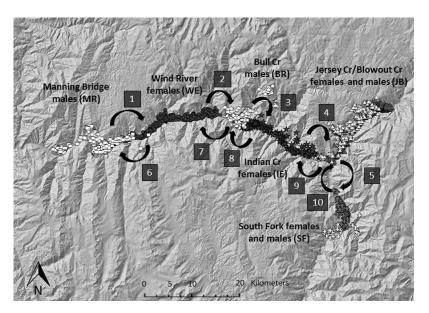

Figure 2. Six social groups of bighorn sheep defined by agglomerative hierarchical cluster analysis in the Salmon River drainage in west central Idaho, USA, 2007–2013. From west to east, the groups are the Manning males (MR), the Wind River females (WE), the Bull Creek males (BR), the Indian Creek females (IE), the Jersey Creek females and the Blowout Creek males (JB; dark and light triangles, respectively), and the South Fork males and females (SF; dark and light pluses, respectively). Also shown is the framework for the spatially explicit multi-state model including 6 areas occupied by social groups of bighorn sheep (MR through SF). Symbols depict locations of collared sheep in each group. Transitions between groups are labeled 1–10.

Table 2. Subset of models of transition probabilities (Ψ) between groups of bighorn sheep in the Salmon River drainage, west central Idaho, USA from 2007–2012. Models are ranked from best to worst based on Akaike's Information Criteria (AIC), difference in AIC (ΔAIC), Akaike weights (w_i), and number of model parameters (K).

Model	K	AIC	ΔAIC	w_i
Ψ(summer + winter + sex + (summer × sex) + (winter × sex))	17	4,161.850	0.000	0.863
Ψ(summer + winter + (summer × sex) + (winter × sex))	16	4,170.040	8.190	0.014
Ψ(summer + sex)	14	4,271.478	109.628	0.000

Creek females; Fig. 2). In contrast to DeCesare and Pletscher (2006), social groups of females along the Salmon River overlapped slightly, but not to the large extent reported by Festa-Bianchet (1986a). Our models of transition probabilities indicated that these low levels of overlap resulted in limited potential for interactions between female groups.

Whereas we observed connectivity among social groups along the Salmon River canyon, connectivity between the Salmon River canyon and South Fork subpopulations was negligible. Even though these groups were separated by <5 km, the probability of transition between the Salmon River canyon and South Fork subpopulation was <1% for females and only 1–5% for males, regardless of season. The relative lack of connectivity we observed could be because we had only 5 radio-collared sheep in the South Fork; therefore, we may not have detected movements out of that area. Alternatively, the Salmon River may be a behavioral or physical barrier to movements of bighorn sheep (Geist 1971, Singer et al. 2000). We observed only 1 of 18 radio-collared males and females from the Jersey-Blowout creek group move into the South Fork group area, suggesting that interaction between these subpopulations was uncommon.

Connectivity can influence the transmission of disease in spatially structured populations by increasing encounter rates between members of different groups (Hess 1996, Crooks and Sanjayan 2006, Mills 2007, Grassly and Fraser 2008, Jesse and Heesterbeek 2011), including those of bighorn sheep (George et al. 2008, Clifford et al. 2009, Sells et al. 2015). Whereas we could not measure encounter rate directly, we measured spatial and behavioral components necessary for encounters between members of different groups (i.e., connectivity). To the extent that our estimates of connectivity reflect actual encounter rates, our work has

implications for spread of pneumonia among social groups within a population of bighorn sheep. Male movements among female groups during the rut would have the greatest potential for transmitting disease in our population. Once disease is introduced, however, the tight-knit structure within female groups and the non-zero probability of transition between these groups could serve to help spread and maintain disease within the population, outside of the rut.

Our results suggest probability of disease transmission from males would be higher during the winter rut when transition probability of males among groups was nearly 3.5 times higher than at other times of the year. Cassirer et al. (2013) found that the odds of pneumonia-caused mortalities of adults were 3 times higher during winter than during the rest of the year, which they hypothesized was the result of increased encounters during the rut (Cassirer et al. 2013). These similarities suggest a potential mechanistic link between movements among groups of bighorn sheep and spread of disease.

For our study, we made the standard open population capture-recapture assumptions. Violation of these assumptions could have resulted in under- or overestimation of connectivity. We did not evaluate the likelihood of disease spread within the Salmon River canyon population directly but assumed a positive relationship between probability of transition, connectivity, and potential disease transmission. If our assumption was invalid, then 1) transition probabilities may not be an adequate index of the contact between groups that can result in transmission of disease, or 2) connectivity may play little role in transmission of disease between social groups of bighorn sheep, contrary to existing hypotheses (Cassirer and Sinclair 2007, George et al. 2008); our results

Table 3. Monthly transition probabilities (Ψ) of bighorn sheep between geographic areas encompassing 6 social groups (MR = Manning Bridge males, WE = Wind River females, BR = Bull Creek males, IE = Indian Creek females, JB = Jersey Creek females and Blowout Creek males, SF = South Fork Salmon females and males) in the Salmon River drainage, in west central Idaho, USA, from 2007–2013.

Transition	Male summer		Male winter		Female summer		Female winter	
	Ψ	SE	Ψ	SE	Ψ	SE	Ψ	SE
MR→WE	0.089	0.005	0.326	0.075	0.071	0.011	0.054	0.135
WE→BR	0.080	0.004	0.296	0.075	0.064	0.010	0.049	0.132
BR→IE	0.287	0.017	0.756	0.068	0.235	0.034	0.183	0.120
IE→JB	0.200	0.011	0.606	0.083	0.161	0.019	0.125	0.154
JB→SF	0.003	0.000	0.013	0.011	0.002	0.001	0.002	0.013
WE→MR	0.095	0.005	0.343	0.079	0.076	0.011	0.058	0.143
BR→WE	0.152	0.009	0.499	0.094	0.122	0.020	0.094	0.160
IE→BR	0.179	0.010	0.563	0.086	0.145	0.018	0.111	0.158
JB→IE	0.118	0.006	0.411	0.080	0.095	0.012	0.072	0.149
SF→JB	0.011	0.001	0.046	0.032	0.009	0.003	0.007	0.039

would thus incorrectly represent likelihood of disease transmission for the bighorn sheep we studied.

We used a multi-state model framework for estimating the probability of transition between bighorn social groups, which was advantageous for a number of reasons. Principally, it is a dynamic measure of connectivity; instead of using joint use of space as the estimated probability that animals from one group will be found in the area occupied by another, our model used locations of individuals within the space occupied by a different group to estimate probabilities of transition of individuals between groups. Further, probabilities between many groups can be multiplied to give an estimate of connectivity across a population. For example, to estimate the probability that a Manning Bridge male will transition into the Indian Creek female group during the winter (Fig. 2), we would multiply the transition probabilities between the groups MR, WE, BR, and IE, i.e., $0.34 \times 0.30 \times 0.76 = 0.08$ (Table 3). Additionally, the model is also adaptable because it enables estimation of transition probabilities on extremely fine (daily) or very large (multi-annual) time scales. Another useful characteristic of a multi-state model framework is its flexibility in data that can be used to populate it (e.g., combining VHF and GPS location data in a staggered entry format). Our approach could be extended to apply to other species that form spatially explicit social groups, exist in a metapopulation structure, or occupy disjunct habitats.

MANAGEMENT IMPLICATIONS

Males that range widely during the rut have the greatest potential for coming into contact with infected conspecific or domestic sheep and spreading disease through a population of bighorn sheep. This potential varies seasonally, allowing land managers to plan grazing of domestic sheep for spring and summer months when males are relatively inactive. Simulations by Hess (1996) predicted that for a linear population consisting of discrete groups, a single patch quarantine (i.e., no movement allowed into or out of an area) reduces the probability of disease transmission. Our work suggests that removal of a social group or management actions that limit movements in and out of that group (e.g., hunting, fencing, habitat manipulations) may reduce the likelihood of disease transmission in a linearly distributed population of bighorn sheep such as we observed. Further work is needed to evaluate the potential efficacy of such actions on bighorn populations where social groups are not distributed linearly.

ACKNOWLEDGMENTS

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