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Bighorn sheep (Ovis canadesis) populations drastically declined throughout North America during the early 1900's, with many populations extirpated from historic ranges. Bighorn reintroductions or supplementations via translocation efforts has been a primary tool used to reestablish and support bighorn sheep. However, translocations are financially, biologically, and logistically challenging, with many bighorn translocation efforts ultimately considered unsuccessful. Because of these challenges, wildlife managers continue to investigate factors that may improve the likelihood of translocation success, including conducting habitat improvements and increasing monitoring efforts of translocated bighorn sheep. Beginning in 2009, translocations of bighorn sheep to the Seminoe Mountains were conducted in south-central Wyoming by the Wyoming Game and Fish Department (WGFD). Bighorns from 3 translocation efforts were released and monitored in the Seminoe area, where no known remnant bighorns remained from previous translocation attempts. Global positioning system (GPS) data recovered from a sample of radio-collared bighorns shortly after translocations revealed bighorns were distributed toward the perimeter of the area intended for occupancy, and it was postulated that habitat improvements through prescribed burning may open restrictive habitat and promote increased bighorn use of the study area. Prescribed burning was scheduled to occur in the study area in 2011. I developed research objectives in relation to bighorn sheep translocations to investigate 1) how long bighorn take to acclimate to new surroundings after translocation events, and 2) provisional impacts of fire-mediated habitat alterations on bighorn distribution, habitat selection, and demography. To achieve my objectives, I monitored bighorn sheep in the Seminoe Mountains from 2009–2013. I also used GPS location data gathered from 40 bighorn sheep (F =

32, M=8) that were radio-collared during initial translocation events from 2009–2011, and after the initiation of habitat alterations in 2011 I gathered additional data from another capture effort in the study area where 25 bighorns (F=20, M=5) were collared and released on site, collecting GPS data through 2013.

In Chapter 2 I conducted an analysis investigating the temporal aspect of bighorn acclimation by measuring the amount of time for daily movement rates to stabilize for each bighorn after being released. I found it took approximately 30 days for bighorns to acclimate after being translocated, but only about 5 days if animals were captured and released in the same area where they were familiar with their surroundings. Also, animals that were released where no extant bighorns existed took 57% longer to acclimate, indicating that releasing bighorns with conspecifics reduces the time it takes to acclimate to novel environments. These findings may assist managers in developing efficient monitoring protocols after bighorn translocations occur.

To accomplish my second objective I used a suite of techniques to analyze bighorn distribution, habitat selection, and bighorn demographics in response to fire-mediated habitat alterations. In Chapter 3 I compared bighorn utilization distribution size, overlap, and similarity across a spectrum of home range contours before and after treatments, identifying how changes occurred across varying home range levels. I found bighorns expanded distributions after fires by approximately 200%, and that core home ranges were altered to a higher degree than full home range extents. In Chapter 4, I next modelled resource selection of bighorns in the study area using a negative binomial general linear regression model to specifically identify if bighorn selected for fire-treated areas. Resource selection models showed no selection for fire-treated areas overall, although mean proportion of bighorn locations within areas treated with prescribed burning increased after treatment, lending some evidence toward selection for prescribed burns.

Finally, in Chapter 4 I compared bighorn fire responses to bighorn survival throughout the study. Kaplan-Meier estimates showed bighorn survival was high early in the study, and I found some support that bighorns that expanded distribution after prescribed burns increased use of treated areas. However, bighorn survival decreased precipitously (~30%) after a wildfire event in 2012 that removed much vegetation and that coincided with severe drought conditions in the study area, delaying plant phenological response into the winter season. This event likely caused bighorns to expand distribution in an attempt to gain access to forage (no habitat selection identified), and bighorns that died in association with poor body condition had higher overlap with burned areas than those that survived. Given these results, it is likely that bighorns may respond positively to small-scale prescribed burns, but that large-scale fires, especially those that coincide with drought conditions and that encompass large areas currently occupied by bighorn sheep, may reduce bighorn fitness. Therefore, it is most likely best to conduct habitat alterations prior to translocation events.

ECOLOGY AND EFFECTS OF FIRE-MEDIATED HABITAT ALTERATIONS FOR BIGHORN SHEEP TRANSLOCATED TO THE SEMINOE MOUNTAINS, WYOMING

By
Justin G. Clapp

A thesis submitted to the Department of Ecosystem Science and Management and the University of Wyoming in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

RANGELAND ECOLOGY AND WATERSHED MANAGEMENT

Laramie, Wyoming
January 2015

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ACKNOWLEDGMENTS

I would like to acknowledge persons whose expertise, guidance, leadership, and friendship helped pave the way for my graduate success. Tom Ryder and Kevin Hurley played essential roles in bighorn translocations conducted by the WGFD, as well as the continuation of the project into my thesis work. I thank my committee chair, graduate advisor, professor, and friend, Dr. Jeff Beck, who graciously took the time and effort to support my project in its infancy, and who provided the opportunity and guidance to make it a reality at the University of Wyoming. My graduate advisor and committee members Dr. Ken Gerow, Dr. Scott Miller, and Dr. Hall Sawyer all contributed greatly to the success of my research by providing insight to research questions and objectives, teaching, assisting with study design and analysis techniques, and coauthoring and reviewing manuscripts. Dr. Shannon Albeke, Dr. Michael Dillon, and Dr. Trent McDonald provided much needed insight in statistical and modeling procedures, as well as effectively fielded the barrage of questions and conundrums I furnished. I am fortunate for a cohort of graduate student comrades whose friendship and support inside and outside the classroom often retained my sanity. I thank the University of Wyoming, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and Wyoming Wild Sheep Foundation for providing funding to support my research. Chris Otto, Mike Murry, and others at the Rawlins BLM Field Office conducted habitat treatments in the Seminoe Mountains that were an essential part of my research. WGFD personnel Greg Hiatt and Bill Brinegar provided both logistical support and field expertise. My friends and colleagues Dan Bjornlie and Dan Thompson provided continuous support throughout my research, and were greatly influential, motivational, and supportive both before and during my study. Finally, I thank my family, and most importantly my wife Malinda.

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CHAPTER 1

INTRODUCTION

Bighorn sheep (*Ovis canadensis*) populations dramatically declined throughout their range in the early 20th century, with multiple populations extirpated from their historical habitats. Efforts to restore bighorn sheep to historical ranges have been ongoing since the early 1900s. A primary obstacle evident in bighorn sheep restoration is that bighorn are poor colonizers (MacArthur and Wilson 1967), and are known to exhibit strong site fidelity to their home ranges after establishing knowledge regarding escape terrain, water sources, and lambing habitat (Geist 1970, 1971; Shackelton et al. 1999). Because they do not readily search for unoccupied habitat, numerous translocation efforts have been undertaken to restore bighorn populations to historical habitat and augment waning populations (Hanson 1980). By 1990, over 50% of all bighorn populations originated from translocation efforts (Bailey 1990), making translocation a key component to bighorn restoration.

Habitat analysis and evaluation play a key role in the success of translocated bighorn sheep populations. Research on habitat suitability and selection should be extensive prior to and after translocations to increase the likelihood of successful translocations because translocations of large animals are known to be time consuming, expensive, and logistically and politically challenging (Beck et al. 1994, Biggins and Thorne 1994, Wolf et al. 1996, Dunham 1997, Fritts et al. 1997). For example, reported costs for the translocation of each bighorn sheep in the United States was \$2,257 in 1990 (Bleich 1990). Increased costs due to inflation raised costs to over \$3,000 per animal by 1999 (Zeigenfuss et al. 2000), and over \$4,000 by 2013 (BLS 2013). Even with the substantial costs associated with the translocation of bighorn sheep, translocation techniques are rarely tested (Morgart and Krausman 1981, Thompson et al. 2001), and only an

estimated 41% of bighorn sheep translocations are considered successful (Singer et al. 2000). Therefore, it is important that wildlife managers continue to evaluate factors influencing translocation efforts to increase the potential for successful bighorn sheep restoration.

STUDY AREA

The Seminoe Mountains, located approximately 40 km (25 mi) north of Sinclair, Wyoming, are one of many mountains that span central Wyoming. These mountains include Bennett, Crooks, Ferris, Green, Seminoe, and Shirley Mountains. Seminoe Mountains are separated from Bennett Mountain to the east by the North Platte River (flowing generally to the north through the range), with two hydroelectric dams (Seminoe and Kortes) within the confines of Seminoe Canyon. The Seminoe Mountains lie on a latitudinal orientation with prominent south and north faces, with the Morgan Creek WHMA in the heart of the mountain range (Fig. 1.1). The WHMA included mountainous terrain on the western side of the North Platte River containing three streams (Cottonwood, Marking Pen, and Morgan Creeks) that converge and flow eastward into the North Platte River below Seminoe Dam. This landscape was variable and included topographical features from vertical canyon walls on the eastern edge, to gentle slopes and long draws and ridges in the west; as well as numerous rock outcrops throughout the area. The headwaters of Cottonwood and Marking Pen Creeks marked the highest elevations at 2500 m, while elevation fell to around 1830 m below Kortes Dam where the North Platte River exited the mountain to the north (Hiatt 1997).

Weather data from the Seminoe Dam area reported an average annual precipitation of 33 cm, with spring seasons contributing the most precipitation. The average annual temperature was 5°C (42 °F), resulting in a short frost free period of 70-90 days, and 45% of annual precipitation

in the form of snowfall. High winds were also common in the Seminoe area, especially in exposed slopes and ridges.

Primary vegetative cover types included sagebrush (*Artemisia* spp.), grassland, and conifer with a mixed shrub understory; but mountain shrub, riparian meadow, and riparian broadleaf cover were also found in the study area. Limber (*Pinus flexilis*), lodgepole (*P. contorta*), and ponderosa (*P. ponderosa*) pines, and Rocky Mountain juniper (*Juniperus* scopulorum) comprised dominant coniferous trees, while deciduous tree species include aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), and narrowleaf cottonwood (*Populus angustifolia*). Dominant shrub species included antelope bitterbrush (*Purshia tridentata*), big sagebrush (*A. tridentata*), and true mountain mahogany (*Cercocarpus montanus*). Common grass species included bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), prairie junegrass (*Koelaria cristata*), and spike fescue (*Leucopoa kingii*). Although pussytoes (*Antennaria rosea*), silvery lupine (*Lupinus argenteus*), and sulphur buckwheat (*Eriogonum umbellatum*) existed in the study area, forbs were poorly represented in most sites (Hiatt 1997).

Mule deer (*Odocoileus hemionus*) were the most abundant ungulate species in the study area; however, elk (*Cervus elaphus*) were also common. The lower elevation foothills surrounding Seminoe Mountain provided habitat for abundant pronghorn (*Antilocapra americana*). The study area also received occasional use by white-tailed deer (*O. virginianus*) and moose (*Alces alces*). Mammalian and avian carnivores included coyote (*Canis latrans*), bobcat (*Lynx rufus*), golden eagle (*Aquila chrysaetos*), mountain lion (*Puma concolor*), and occasionally black bear (*Ursus americanus*; Hiatt 1997).

BACKGROUND

Bighorn translocation efforts in the Seminoe Mountains were initiated in 1958 and continued through 1985. These efforts entailed releasing 237 individuals through 6 separate translocations (Hiatt 1997). Despite these extensive efforts, reestablishing bighorn sheep in the Seminoe Mountain area remained unproductive. However, recent evidence suggested that successful bighorn restoration is most likely to occur when habitat conditions and phenology of life-history strategies (i.e., timing of migration and lambing) of the source population match those of the target population (Douglas and Leslie 1999, Kauffman et al. 2009). For example, Singer (2000) reported that using indigenous source herds doubled the likelihood of successful bighorn translocations. Initial Seminoe bighorn translocations (1958, 1967, 1978, 1980, and 1985) used source animals from the high-elevation Whiskey Mountain herd near Dubois, Wyoming. Migratory bighorns from the Whiskey Mountain herd have adapted to seasonal climatic variations in the Wind River Mountains by migrating along elevational gradients ranging from 2193 to 3473 m as they enter and leave winter range. As part of this life-history strategy, bighorn sheep from Whiskey Mountain typically lambed from late-May to mid-June, such that lambing coincided with peaks in vegetative green-up. When translocated into the lower-elevation Seminoe Mountains where green-up occurred earlier (mid-April through early-May), these animals initiated lambing when herbaceous vegetation was already beginning to senesce. This lack of birth pulse synchrony with vegetative green-up presumably resulted in poor nutrition for lactating ewes and low lamb survival for the descendants of these early translocation efforts (Kinter et al. 1992). As a result, population estimates for the Ferris and Seminoe Mountains declined to fewer than 15 animals by 2009 (Sawyer et al. 2011).

Recent translocation efforts by the Wyoming Game and Fish Department (WGFD) were conducted to ensure that habitat conditions for the source population match those of the release area. Translocations of low-elevation, non-migratory bighorn sheep from Oregon and Montana appeared to be successful in Devil's Canyon (Kauffman et al. 2009) of north-central Wyoming and the Laramie Range of southeastern Wyoming (Sawyer et al. 2009), where forage phenology matched the birth-pulse of low elevation bighorn sheep. These translocation efforts indicated that deficiencies in suitable forage quality following lambing could be indirectly compensated for by introducing bighorn sheep from source herds adapted to lamb earlier to match vegetative greenup. Under this model, the WGFD began translocation efforts in the Seminoe Mountains on 2 December 2009 when 20 non-migratory bighorns (M = 5, F = 15) from the Diablo Mountains in south-central Oregon were released into the Morgan Creek Wildlife Habitat Management Area (WHMA) near the center of the Seminoe Mountains. This release was followed with the translocation of 12 bighorns (M = 3, F = 9) from the Devil's Canyon herd (north-central Wyoming) on 30 January 2010. Bighorns were equipped with GPS collars from these releases and were monitored throughout the winter and lambing season of 2010. On 2 December 2010, 20 additional bighorns (M = 4, F = 16) were translocated to the Seminoe Mountains from the John Day River Canyon in central Oregon. In total, these 3 translocation efforts in 2009 and 2010 resulted in releasing 52 bighorns (M = 12, F = 40) into the Seminoe Mountains, with 40 of these sheep equipped with GPS transmitters. My observational data indicated newly translocated bighorns had higher lamb survival rates compared to previous translocation efforts in the Seminoe Mountains (Table 1.1), where lambing data collected in 1985 indicated as few as 1 lamb observed surviving to fall (Hiatt 1997).

Initial Habitat Selection Patterns of Translocated Bighorn Sheep

Sawyer et al. (2011) modeled distribution and habitat selection patterns for 16 GPS-collared bighorns in the Seminoe Mountains from December 2009 through June 2010. These models indicated that bighorns appeared to select only portions of available suitable habitat on winter ranges (Sawyer et al. 2011). Results showed preliminary distribution and habitat selection patterns among translocated individuals, and formed the basis for posing my research questions concerning habitat usage, as well as providing pre-fire distribution data. GPS locations for most translocated sheep showed a pattern of habitat use along the perimeter of the study area, avoiding large areas of predicted high use habitat throughout the winter (Fig. 1.2). It was postulated that prescribed fire may provide greater accessibility to portions of the unused habitat, especially within 200 m of escape terrain (Sawyer et al. 2011).

FIRE-MEDIATED HABITAT ALTERATIONS

Land managers asserted that foraging areas inside the primary burn area in the Seminoe Mountains were not productive due to lack of disturbance and/or herbivory (Bureau of Land Management [BLM] 2011). Specifically within the Morgan Creek WHMA there had been no permitted livestock grazing since 1965 (BLM 2011). According to the BLM, shrub over maturity, decadence, and a lack of structural and age stratification contributed to a decrease in habitat quality in the Seminoe area. Grasses and forbs that were important for foraging wildlife populations in the area had shown a reduction in overall biomass, vigor, and nutritional quality due to competition from shrub communities (BLM 2011). Also, many areas on the south face of Seminoe Mountains had been encroached by limber and ponderosa pine and Rocky Mountain juniper. In testing a habitat evaluation procedure for Rocky Mountain bighorn sheep, Johnson and Swift (2000) concluded that barriers caused by dense vegetation and that limited bighorn

visibility had the most pronounced influence on core habitats across all of their study areas in Colorado, which suggested that prescribed fires in the Seminoe Mountains may expand bighorn sheep utilization of habitat previously not selected by bighorn sheep.

Prescribed burning was initiated by the Rawlins BLM Field Office during the first week of May 2011. Although the Seminoe Mountains were entirely included in the Marking Pen Creek Prescribed Burn Project, the primary treatment area included the majority of the south face of the mountains, spanning northerly to include the southern portion of the Morgan Creek WHMA. Since the timing of the burn coincided with lambing dates expected for a majority of translocated ewes on the south side of the Seminoe Mountains, the WGFD and the Rawlins BLM delineated a portion of the area designated as the 2010 lambing habitat to be excluded from the primary treatment area in an attempt to avoid disturbances on ewes during lambing. This burn targeted older, established forage, as well as encroaching timber stands that limited visibility and movement of bighorn sheep. A fire line was established along the eastern edge of the target area, following the Cottonwood and Marking Pen drainages through the Morgan Creek WHMA to distinguish the northern boundary of the burn. Helicopter crews then initiated the ignition source that focused on the southern rim of the mountain, as well as the southern portion of the Morgan Creek WHMA. Timing of the burn (spring ignition) resulted in a mosaic burn pattern around snow cover and low fuel load areas.

Because specific areas were intentionally avoided to reduce impacts on bighorn sheep during lambing in spring 2011, the BLM scheduled an additional prescribed fire, using existing fire lines, to include much of the lambing areas that were initially avoided. This fire, scheduled to occur in fall 2011, was not implemented until the following spring (March 2012). The 2012 prescribed burn occurred before initiation of lambing by bighorn ewes, and targeted the mid to

low-slope areas of the southern edge of the Seminoe Mountains. The 2012 prescribed fire burned from the southern edge of the 2011 fire and expanded the treatment area toward the south. Much of this burn targeted lower elevation stands of forage as well as limestone faces of the slope occupied by areas of dense true mountain mahogany and Rocky Mountain juniper. This fire concluded the BLM's Marking Pen Creek Prescribed Burn Project for the Seminoe area which included approximately 7.5 km (1,853 ac) of burned area.

An unexpected wildfire occurred in the study area in July 2012. This lightning initiated wildfire burned a large area (approximately 12.6 km² or 3,113 ac) of the northern portion of the mountains, potentially affecting bighorns that utilize that portion of the study area. In total, three separate fires occurred between 2011 and 2012; two of which were prescribed (one fire each spring on the southern portion of the mountain) and one wildfire (summer 2012 on the northern portion of the mountain), totaling around 20.1 km² (4,966 ac) burned (Fig. 1.1).

RESEARCH OVERVIEW

My study expanded monitoring and data collection from bighorn sheep through 2013 to address the influence of fire relative to suitable habitat with before and after data used to assess responses from the newly established bighorn sheep population, and compared post-release acclimation periods for translocated bighorn sheep. On 2–3 December 2011, 20 F and 5 M bighorns were captured in the study area via helicopter net-gunning, processed, and released on-site throughout the study area following University of Wyoming Institutional Animal Care and Use Committee approved protocols (protocol 12012011) and Wyoming Game and Fish Department Chapter 33-750 permit. Biological samples were taken from each captured bighorn for disease and parasite screening, and 25 refurbished GPS collars (Telonics = 4, ATS = 21) were deployed on these bighorns to collect location data every 5 hours for 18 months until they remotely detached in

June 2013. Captured bighorns that were previously collared and released in translocation efforts (n = 16) were identified, and metal ear tags were inserted into both ears of 5 bighorns born in the Seminoe Mountains that were never previously captured. Four bighorns captured in December 2011 were not GPS-collared when translocated to the Seminoe Mountains. This capture effort collected additional location data from bighorn sheep in the study area after fire events, and was essential to accomplish my research objectives.

Translocation efforts often result in elevated stress to animals as they seek out suitable habitat after being released into novel environments. The time associated with highly variable movements often accompanied with heightened mortality risk has been termed "acclimation period," and protocols are often implemented to monitor recently released animals during this time. My research began with an analysis to quantify acclimation periods of translocated bighorn sheep after releases, informing efficient timeframes for monitoring released bighorns and providing protocols that ensure potentially biased location data are properly censored before being used in subsequent analyses.

Another focus of my research was to assess the effects of prescribed burning and wildfire on bighorn sheep. I began by using multi-seasonal GPS location data to compare home range distributions before and after fires to assess impacts of fire-treated habitat on bighorn sheep occurrence. I calculated a variety of comparative statistics between paired home range utilization distributions to identify alterations including relative changes in home range size, home range overlap and expansion, and home range similarity. Because home range comparisons may vary depending on the chosen home range contour used for comparison, I compared across a spectrum of levels and summarized data as trends across increasing home range contours. I also used this method to quantify home range overlap with treated areas after habitat alterations occurred.

I used GPS location data to build seasonal habitat selection models as a tool to identify if bighorn sheep selected for burned habitats after treatments (while incorporating other habitat variables known to influence bighorn occurrence) in a multiple regression resource selection function (RSF) framework. In addition, I conducted paired *t*-tests for collared sheep sampled before and after fire to identify significant differences in the proportion of locations that overlapped individual fire events as an indicator of selection for specific types of habitat treatment (prescribed fire and wildfire). With the information gathered on bighorn distribution alterations, overlap with treated areas, and habitat selection, I used field-documented cause-specific mortality to model bighorn survival and to conduct various analyses that linked demographic response (survival) of bighorns with various responses to fire-mediated habitat alterations throughout the study period.

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Table 1.1. Ground observations of lambing success in the spring and lamb survival in fall seasons for bighorn sheep in the Seminoe Mountains, Wyoming, USA, 2010–2013. No fall observations were conducted in 2011.

Season	Mature females observed	Lambs observed	Lamb/female ratio	Fall lamb survival
2010				0.83
Spring	20	12	0.60	
Fall	20	10	0.50	
2011				NA
Spring	30	12	0.40	
Fall	NA	NA	NA	
2012				0.63
Spring	25	14	0.56	
Fall	26	9	0.35	
2013				NA
Spring	21	13	0.62	

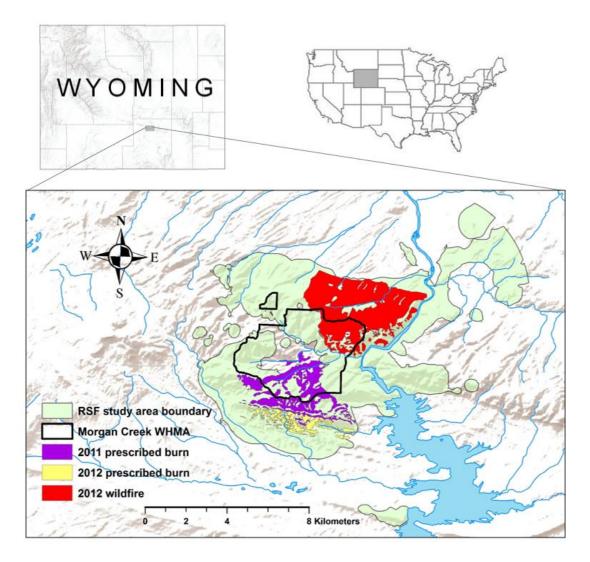


Figure 1.1. Study area map including WHMA and RSF study area boundaries and fire events from 2011–2012 in the Seminoe Mountains, south-central Wyoming, USA.

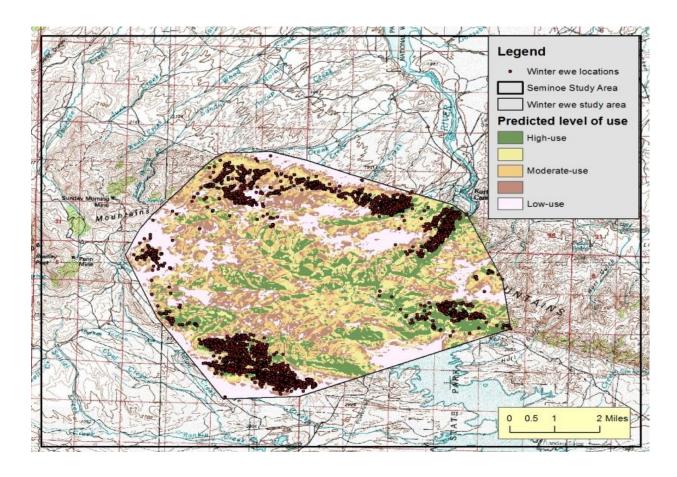


Figure 1.2. Winter ewe locations (n = 17,241) overlaid on RSF model predictions for winter 2009–2010, Seminoe Mountains, Wyoming (Sawyer et al. 2011).

CHAPTER 2

POST-RELEASE ACCLIMATION OF LOW-ELEVATION, NON-MIGRATORY BIGHORN SHEEP

Published in The Wildlife Society Bulletin 38:657-663

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ABSTRACT Use of global positioning system (GPS) transmitters provides opportunities to evaluate ecological questions associated with fine-scale animal movements. One important application is to evaluate how animals acclimate to new surroundings after translocation. Our objective was to quantify temporal acclimation for low-elevation, non-migratory bighorn sheep (*Ovis canadensis*) from 3 translocations to the Seminoe Mountains in south-central Wyoming, USA, from 2009 to 2010 (n = 38) as well as for bighorns captured and released on-site in 2011 (n = 24). We used number of days for movements from individual bighorn to stabilize as a measure of acclimation. Mean acclimation for translocated bighorns after release was 29.3 days (SE = 2.5, range = 0–70). Mean acclimation for bighorns captured and released on-site was 5.0 days (SE = 2.4, range = 0–52). Paired comparisons indicated acclimation for 16 previously translocated bighorns that were captured and released on-site was reduced by 30.8 days (SE = 5.0) or 86%.

Within translocation efforts, bighorn females in supplemental releases acclimated an average of 19.5 days sooner (or in 57% of the time) than animals from the first translocation. Because acclimation periods after translocation releases are associated with increased mortality risk, managers should consider supplemental releases to minimize acclimation periods.

KEY WORDS acclimation, bighorn sheep, data-censoring, functional data analysis, global positioning system, GPS, movement rate, *Ovis canadensis*, translocation, Wyoming.

The increasing availability of high-resolution global positioning system (GPS) location data for wildlife populations has provided opportunities to investigate ecological questions associated with fine-scale animal movements. One useful application of these data is to document how animals acclimate to new surroundings directly after translocations. Dispersal has been described as movement of one or more individuals away from the area or population where they were born to a new area where they settle and reproduce (Croteau 2010). However, movements after translocation are unlike dispersal because these movements are not related to an animal's natural and deliberate behavior (Letty et al. 2007). Mortality often increases directly after captured animals are released because of stresses associated with translocations (Dickens et al. 2010). The duration of this increased mortality risk after release has been defined as "acclimation period" (see Hamilton et al. 2010). In many cases, the intensity of movement (i.e., distance, frequency, and propensity) is high directly after release as animals explore new environments (Rittenhouse et al. 2007, Hester et al. 2008). This can be costly to animals, resulting in a decrease in foraging behavior, predator vigilance, and reproductive effort—leading to decreased survival and reproductive success—and in turn, a reduction in the probability of population establishment

(Letty et al. 2000, LeGouar et al. 2012). Hofer and East (1998) and Creel (2001) document varying responses to stress induced by translocations according to multiple characteristics such as age, social status, sex, and physical condition, and the probability of animals successfully settling into a release area likely differs among individuals (Letty et al. 2007). Furthermore, some species are readily attracted to conspecifics in resident populations following release into new environments (Stamps 1988, Boulinier and Danchin 1997).

Initial locations from captured and released animals are often censored to ensure that biased locations are not included in subsequent analyses. For instance, White and Garrott (1990) recommended omitting location data up to 1 week after capture to account for post-release acclimation. When capturing, immobilizing, and releasing white-tailed deer (*Odocoileus virginianus*) on-site, Dechen Quinn et al. (2012) reported that decreased movements of individuals during acclimation after capture were ephemeral, with most individuals resuming normal movement patterns within 14 days. However, when translocated into new environments, animals have a tendency to exhibit highly sporadic and increased movement rates for extended periods of time before settling (Hunter 1998, Moehrenschlager and Macdonald 2003, Bennett et al. 2012). The removal of biased location data due to effects of capture, immobilization, or translocation of animals is often accomplished by visual inspection of the location data, but may be difficult to quantify (Dechen Quinn et al. 2012).

Efforts to restore bighorn sheep (*Ovis canadensis*) throughout North America have been ongoing since the early 1900s, with numerous translocation efforts undertaken to restore populations to historical habitat and augment waning populations (Hansen 1980). A substantial portion of current bighorn populations originated from translocation efforts (Bailey 1990, George et al. 2009, WAFWA 2013), making translocation a key component of bighorn restoration.

Efforts are often implemented to monitor bighorns after translocations, which can accrue notable costs associated with both ground and aerial monitoring. Monitoring efforts may be implemented to observe or record animals wandering onto roadways, into surrounding areas where interactions with domestic animals are likely, or to document individuals leaving the habitat intended for occupation. Monitoring efforts are also implemented because released animals suffer higher mortality rates than those in established, wild populations (Craven et al. 1998). Increased predation of translocated animals (Yoder et al. 2004, Letty et al. 2007) may also influence the potential for successful bighorn establishment, and multiple studies report high vulnerability to predation in small bighorn populations, as well as setbacks in reintroduction efforts because of population declines due to predation (Broadbent 1969, Kilpatric 1982, Creeden and Schmidt 1983, Krausman et al. 1999). Estimating bighorn acclimation periods after translocation provides the ability to identify timeframes of increased mortality risk after releases, as well as to maximize effectiveness in monitoring efforts. Even with the substantial costs associated with the translocation of bighorn sheep, only an estimated 41% of bighorn sheep translocations are considered successful (Singer et al. 2000). Therefore, it is important that wildlife managers continue to evaluate factors influencing translocation efforts to increase the potential for successful bighorn sheep restoration.

Our objective was to estimate acclimation periods of low-elevation, non-migratory bighorn sheep by comparing dynamic bighorn movements directly after release to relatively stable movements when bighorns settled into new environments. We predicted acclimation periods of newly translocated bighorns to be longer than those in an on-site capture and release scenario. When examining scenarios that incorporate multiple bighorn releases as in the Seminoe Mountains, we also predicted acclimation periods to be reduced for animals in supplemental

releases because of positive interactions with conspecifics already established in the area.

STUDY AREA

The Seminoe Mountains (106°56′0.000″W, 42°10′0.000″N) are a low-elevation (1,830–2,500 m) range located approximately 40 km north of Sinclair, Carbon County, Wyoming, USA, that encompass 80% federal, 10% state, and 10% private lands. The Seminoe Mountains form one of several independent ranges in south-central Wyoming that were historically inhabited by bighorn sheep (Beuchner 1960, Rea 2006). The Seminoe Mountains are separated by the North Platte River, flowing generally to the north through the range, with 2 hydroelectric dams (Seminoe and Kortes, respectively) within the confines of Seminoe Canyon. The Seminoe Mountains lie on a latitudinal orientation with prominent south and north faces, with the 16.7-km² Wyoming Game and Fish Department's Morgan Creek Wildlife Habitat Management Area positioned in the center of the mountain range. The Wildlife Habitat Management Area included mountainous terrain on the western side of the North Platte River containing Cottonwood, Marking Pen, and Morgan Creeks that converge and flow eastward into the North Platte River below Seminoe Dam. Topographical features in the Seminoe Mountains varied from vertical canyon walls on the eastern edge, to gentle slopes and long draws and ridges on the west, as well as numerous rock outcrops throughout the mountain range.

Primary vegetation cover types included sagebrush (*Artemisia* spp.), grassland, and conifer with a mixed shrub understory intermixed with mountain shrub, riparian meadow, and riparian broadleaf cover types. Limber (*Pinus flexilis*), lodgepole (*P. contorta*), and ponderosa (*P. ponderosa*) pines, and Rocky Mountain juniper (*Juniperus scopulorum*) comprised dominant coniferous trees. Deciduous tree species included aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), and narrowleaf cottonwood (*Populus angustifolia*). Dominant shrub species

included antelope bitterbrush (*Purshia tridentata*), big sagebrush (*A. tridentata*), and true mountain mahogany (*Cercocarpus montanus*). Hiatt (1997) provided lists of common grass and forb species for the study area. Our study area received a 30-year (1981–2010) average annual precipitation of 36 cm, with most precipitation occurring in spring (Western Regional Climate Center 2013). The 30-year (1981–2010) average annual temperature was 7° C (44° F), resulting in a short frost-free period of 70–90 days with 45% of annual precipitation falling as snow (Western Regional Climate Center 2013). High winds were common in the Seminoe area, especially on exposed slopes and ridges.

Mule deer (*Odocoileus hemionus*) were the most abundant ungulate species in the study area; however, elk (*Cervus elaphus*) were also common. The lower elevation foothills surrounding Seminoe Mountain provided habitat for abundant pronghorn (*Antilocapra americana*). Mammalian and avian carnivores included bobcat (*Lynx rufus*), coyote (*Canis latrans*), golden eagle (*Aquila chrysaetos*), mountain lion (*Puma concolor*), and occasionally black bear (*Ursus americanus*).

METHODS

Capture and Translocation of Bighorn Sheep

Despite multiple bighorn translocation efforts from 1958 to 1985 (Hiatt 1997), no known extant bighorns remained in the Seminoe Mountains prior to translocation efforts in 2009–2010 (G. Hiatt, Wyoming Game and Fish Department, personal communication). Low-elevation, non-migratory bighorn sheep were specifically chosen for translocation from source herds that occupied similar habitats and that exhibited life-history strategies (e.g., lambing chronology) congruent with habitat conditions in the Seminoe Mountains (Douglas and Leslie 1999, Kauffman et al. 2009). On 2 December 2009, 20 bighorns (15 F, 5 M) were released in the

Seminoe Mountains from captures that occurred in the Diablo Rim and Coglan Butte areas in Lake County, central Oregon, USA. On 30 January 2010, 12 bighorns (9 F, 3 M) were translocated to the Seminoe Mountains from Devils Canyon in Big Horn County, north-central Wyoming. Finally, on 2 December 2010, 20 bighorns (16 F, 4 M) were released from captures that occurred in the John Day River Canyon in Wasco County, north-central Oregon. These 3 translocation efforts resulted in 52 bighorns released into the Seminoe Mountains from 2009 to 2010. All bighorns were captured via helicopter net-gunning, and were handled, marked, and translocated following state agency (Oregon Department of Fish and Wildlife, see Foster [2005]; Wyoming Game and Fish Department, Chapter 10-1535 and Chapter 33-750 permits) approved protocols.

After capture, bighorns were restrained using front and rear leg hobbles and blindfolded to minimize stress during processing. Each animal underwent a physical examination by trained animal handlers or a state veterinarian; this included documentation of age, sex, and physical abnormalities. Biological samples were taken from each captured bighorn for disease and parasite screening. Self-piercing metal or plastic ear tags were inserted in both ears of captured bighorns unless previous ear tags were evident. Forty store-on-board GPS neck collars (*n* = 13, GEN III, model TGW3500 collars [Telonics, Inc., Mesa, AZ]; *n* = 27, model G2110D [Advanced Telemetry Systems, Isanti, MN]) were affixed to 31 F and 9 M bighorn sheep translocated to the Seminoe Mountains. Twenty-two collars were configured to upload 1 GPS location every hour for 6 months, whereas 18 collars collected 1 GPS location every 5 hours for 18 months. Differences in collar fix rates assisted in providing high-frequency location data as well as extended data given limited battery life of GPS collars. All bighorns were held overnight to accommodate transit time and to ensure all releases occurred during midday hours. Release

sites for bighorns translocated to the Seminoe Mountains were focused within 2.8 km near the center of the study area (Fig. 2.1). Global Positioning System data were collected from translocated bighorns through spring 2011. On 2–3 December 2011, 25 refurbished GPS collars (Telonics = 4, ATS = 21) were attached to 20 F and 5 M bighorns captured and released on-site throughout the Seminoe study area following University of Wyoming Institutional Animal Care and Use Committee approved protocols (protocol 12012011) and Wyoming Game and Fish Department chapter 33-750 permit. Additionally, the same capture company was contracted to conduct all areal captures throughout the study. Biological samples were taken from each captured bighorn for disease and parasite screening. Captured bighorns that were previously collared and released in translocation efforts (n = 16) were identified from existing ear tags, while metal ear tags were inserted into both ears of 5 bighorns born in the Seminoe Mountains that were never previously captured. Four bighorns captured in December 2011 were translocated individuals that were not previously collared, as identified by existing ear tags. Collars attached to these bighorn sheep collected location data every 5 hours for 18 months until they remotely detached in June 2013.

Data Analysis

We estimated individual daily movements (m/day) by calculating straight-line distances between successive locations, rendering l-1 step lengths for each bighorn where l= total number of locations; we subsequently summed step lengths that fell within each day (Harris et al. 1990, Johnson et al. 2002, Dechen Quinn et al. 2012, Rowcliffe et al. 2012). To increase accuracy in daily movement estimates, we allocated the hourly proportion of any step length that overlapped a 24-hour period to the appropriate day. For example, if a GPS unit set to collect location data every 5 hours logged a location at 2200 hours on Day 1 and again at 0300 hours on Day 2, 0.40

of the step length was added to Day 1 and 0.60 was added to Day 2.

Fix rates differed (i.e., 1 or 5 hr) among collared bighorns, yielding different individual daily movement estimates (Rowcliffe et al. 2012). Differences were also observed in daily movement estimates independent of fix rate frequency >1 year after release, indicating variability in routine movements among bighorns. Therefore, we identified acclimation time relative to each individual regardless of actual distance moved. We justified the ability to detect change in movement variation utilizing different fix rates with a 2-tailed, 2-sample t-test, which revealed no significant difference in acclimation periods using data collected with 1-hour or 5-hour GPS fix rates ($t_{36} = 0.80$, P = 0.429).

We employed a functional data analysis (Zhao et al. 2004) to determine individual bighorn acclimation periods from consecutive daily movement estimates. Functional data analysis can be applied using longitudinal data where complex analyses (e.g., random effects modeling, repeated measures analyses) may be avoided by reducing multiple longitudinal responses into a summary measure analysis (Everitt 2002, Ramsey and Schafer 2002). This is done by fitting a function to each experimental unit and subsequently performing appropriate statistical tests on the functions or specific characteristics (summary measures) of the functions. In this scenario, the summary measurement consisted of the time elapsed to reach a value or threshold that indicated settling by the animal (Everitt 2002).

We visually identified stable movement durations from daily movement estimates within the first 180 days after release, and censored 10% of the durations from the beginning and end of these dates to ensure conservative estimates (Fig. 2.2A). The standard deviation (SD) of the stable movement duration was used as a benchmark; each animal was deemed to have acclimated when the SD among daily movements (in moving 5-day windows) reduced to within 75% of the

SD among daily movements in the stable movement duration and stayed settled for 30 consecutive days. We excluded any movements that resulted in variation outside the threshold for ≤5 days because of stochastic factors that may sporadically influence bighorn movements (e.g., aircraft disturbances, anthropogenic proximity, escaping predation, weather events). This process resulted in a summary measurement of number of days to acclimate after release for each bighorn sheep (Fig. 2.2B).

We examined individual or group characteristics such as initial versus supplemental releases, sex, and source herd using independent 2-sample *t*-tests. Because 16 of 25 bighorns captured in the study area were radio-collared upon translocation, the comparison that included translocated bighorns captured and released on-site within the study area was conducted with a paired *t*-test. Prior to all tests, we visually assessed normality of residuals and conducted Levene's test for equality of variances (O'Brien 1981). If the assumption of equal variance was not met, we conducted *t*-tests assuming unequal sample variances. We set alpha levels at 0.05 for all statistical tests and report raw mean, standard error, and range for each estimate. Because we estimated acclimation individually (each bighorn as an experimental unit), we provided standard boxplots for visual representation relevant to sampling distributions, which include median lines, interquartile ranges, and outliers. We conducted statistical analyses with Minitab 16.2.3 (Minitab, Inc., State College, PA) and R 2.15.3 (R Development Core Team 2012).

RESULTS

Between 2009 and 2010, 40 of 52 (77%) bighorns translocated to the Seminoe Mountains were equipped with GPS-collars. Of these bighorns, 13 (F = 10, M = 3) were released in December 2009, 12 (F = 9, M = 3) in January 2010, and 15 (F = 12, M = 3) in December 2010. Our total sample thus consisted of 65 GPS-collared bighorns (including 25 bighorns captured and released

on-site in December 2011). We successfully retrieved transmitters from 64 of 65 GPS-marked individuals. One GPS collar malfunctioned after deployment, yielding no usable data. One bighorn died within 7 days of release, with necropsy indicating mortality due to capture myopathy. All other study animals (n = 62) survived >60 days post-release and were included in subsequent analyses.

Movement rates (m/day) for all bighorn sheep increased during acclimation under translocation and capture–release scenarios (e.g., Fig. 2.2A). We estimated acclimation periods for bighorn cohorts released in translocation efforts and captured and released on-site (Fig. 2.3A), for translocated females and males (Fig. 2.3B), and for translocated females from 3 different release efforts (Fig. 2.3C). Average acclimation period for bighorns released in translocation efforts (n = 38) was 29.3 days (SE = 2.5, range = 0–70). Bighorns captured and released on-site (n = 24) showed an average acclimation period of 5.0 days (SE = 2.4, range = 0-52). A paired t-test revealed mean acclimation time for 16 translocated bighorns (mean = 36.0days, SE = 4.5, range = 9–70) that were recaptured and released on-site (mean = 5.2 days, SE =3.2, range = 0–52) was reduced by 30.8 days (SE = 5.0) or 86% (t_{15} = 6.15, $P \le 0.001$). No difference was found between bighorns born in the study area (n = 5) and the 19 bighorns that had been involved in previous captures ($t_6 = 0.04$, P = 0.967). Within translocation efforts, mean acclimation period for females (n = 29) and males (n = 9) was 31.7 days (SE = 2.9, range = 0-70) and 21.4 days (SE = 3.9, range = 0-37), respectively, yielding no difference in acclimation periods between sexes ($t_{36} = 1.82$, P = 0.077). Mean acclimation for females released in the initial translocation effort (n = 9) was 45.1 days (SE = 6.0, range = 25–70), while the second (n = 9)9) and the third (n = 11) releases yielded mean acclimation of 21.7 days (SE = 4.4, range = 0–32) and 28.9 days (SE = 1.8, range = 23-32), respectively. Females from combined supplemental

releases (i.e., second and third releases; n = 20) acclimated 19.5 days sooner (57% of the time) than those from the initial translocation effort ($t_{10} = 3.05$, P = 0.006; Fig. 2.4). However, we found no difference in acclimation time of females from differing source herds in supplemental releases ($t_{18} = 1.79$, P = 0.099); also the only comparison where different numbers of bighorns were released.

DISCUSSION

Our results supported our prediction that mean acclimation for bighorn translocation releases would be longer in duration than those captured and released on-site. These results showed that releasing bighorns into novel environments increases dynamic movements as they seek out suitable habitats. The most profound difference in acclimation after translocation was identified between translocations involving initial and supplemental releases, where supplementally released bighorns most likely settled in response to attraction to conspecifics already established in the release area. This finding provided strong support for our second prediction. Bighorns in the 3 translocation releases were obtained from differing source herds in Oregon and Wyoming; however, no difference in acclimation for supplemental releases that included bighorns from Wyoming (second translocation) or Oregon (third translocation) indicated it was unlikely that source herd influenced post-release acclimation times. When considering the potential influence of the timing of releases, we remind the reader that only one release effort did not occur on 2–3 December (occurring during the same winter season on 30 Jan 2010), and with individuals exhibiting acclimation periods similar to the other supplemental release.

We did not investigate the effect of release area size or the spatial distribution of resources within the release area that may influence translocated bighorns as they acclimated to new surroundings, and translocating bighorns into larger study areas may increase acclimation

periods because of increased available habitat for bighorns to explore after release. A variety of potential influences (e.g., suitable habitat, predator densities, proximity to domestic livestock, availability of water sources) should be carefully considered prior to any translocation effort. In particular, extensive disease testing should be conducted from potential source herds to avoid the translocation of infected animals. However, if shortening acclimation reduces extensive, spatially broad investigations of novel environments after release, it may also reduce the likelihood of domestic livestock interactions and disease contraction during acclimation.

Calculating precise animal movements depends largely on the ability to acquire fine-scale GPS location data. However, even with improvements in data storage and battery life that are common in contemporary GPS technology, movement rates of animals are typically underestimated due in part to limitations in frequencies of fix rates (Pépin et al. 2004). For example, Rowcliffe et al. (2012) concluded typical telemetry studies would underestimate actual distances travelled by between 67–93%. Although fix rate frequencies continue to be problematic for research involving the census of animal movement rates, identifying relative change in movement rates seems an applicable approach to identify acclimation period for low-elevation, non-migratory bighorn sheep after translocation releases, and can be accomplished using differing fix rates up to 5 hours.

Other statistical methods for documenting acclimation period of ungulates consist of comparing the deviation between annual population-level average daily movement rates and post-release movements (see Dechen Quinn et al. 2012). In our study, functional data analysis enabled us to estimate acclimation periods from GPS data with differing fix rates, without the need to standardize individual movement rates to create a population average. We were also able to estimate acclimation periods without the need to collect location data across multiple years to

establish average movement rates for each calendar day. Finally, Dechen Quinn et al. (2012) report that improper data censoring caused significant differences in movement estimate analyses when using data sets of <90 days. Because we used a summary measurement for each experimental unit, acclimation time was identified for each animal, providing the ability to incorporate individual variation during data-censoring. The ability to censor data for each experimental unit is especially beneficial when analyzing short data sets.

Although other studies document decreases in movement rates after capture and chemical immobilization of various species (Cattet et al. 2008, Dechen Quinn et al. 2012), we identified a consistent increase in movement rates for translocated bighorn sheep after release as well as those captured and released on-site, indicating reduced movement rates after capture may be attributed to residual effects of chemical immobilization. Because of the increased time taken for bighorn movements to stabilize after translocation, and because no bighorns were immobilized in our study, the documented increase in movement rates were most likely attributable to bighorns investigating novel environments to successfully establish home ranges that meet habitat requirements.

MANAGEMENT IMPLICATIONS

We recommend that managers invested in the restoration of bighorns into low-elevation ranges consider both timing and release strategies when planning bighorn translocations. Recognition of the increased risk of mortality associated with bighorn acclimation suggests managers minimize acclimation periods and focus bighorn monitoring efforts during that time. To decrease acclimation periods, we recommend augmenting waning bighorn populations prior to complete extirpation of residents to allow newly translocated bighorns to positively associate with conspecifics. Our results indicated that supplemental releases significantly reduced acclimation

periods of translocated bighorn sheep. Thus, if multiple translocations are planned to reestablish extirpated populations, it may be beneficial to initially release a small group of bighorns to more efficiently assess where they seek suitable habitat, and then conduct larger subsequent releases within a reasonable distance from these animals. We recommend conservative monitoring efforts be implemented to assess acclimation of bighorns translocated to new environments. Although we estimated mean acclimation time approximately of 30 days after releases, individual acclimation ranged from 0 to 70 days, indicating that individual behaviors or site conditions may lead to variable acclimation times. Furthermore, biologists acquiring GPS data for use in subsequent analyses should consider identifying acclimation periods of translocated animals individually.

ACKNOWLEDGMENTS

We thank S. E. Albeke, L. A. Varelas, J. D. Clapp, K. T. Smith, and K. L. Taylor for excellent support in both data management and analysis techniques. G. S. Hiatt and B. A. Brinegar, Wyoming Game and Fish Department, provided exceptional logistical and field support. We thank France Flying Service and Sky Aviation, as well as local landowners, for logistical support. The University of Wyoming, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and Wyoming Wild Sheep Foundation provided funding.

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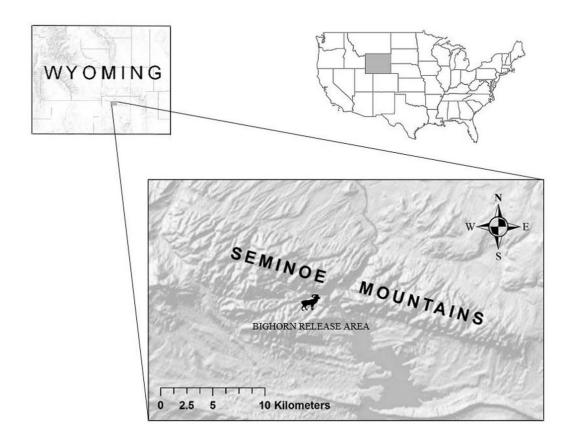


Figure 2.1. Study area for low-elevation, non-migratory bighorn sheep translocations on 2 December 2009 (n = 20), 30 January 2010 (n = 12), and 2 December 2010 (n = 20) in the Seminoe Mountains, Wyoming, USA. Bighorn silhouette represents the general release area for all translocation releases.

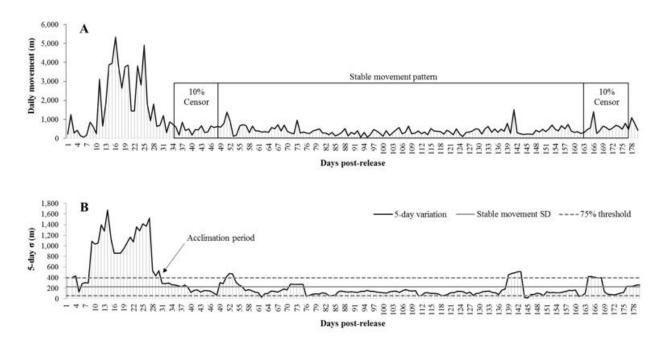


Figure 2.2. Summary measurement (acclimation period) from function applied to post-release daily movements of a bighorn female translocated on 2 December 2010 to the Seminoe Mountains, Wyoming, USA. (A) Visual estimation of stable movements from total daily movement rate (m/day) to 180 days after release. (B) 5-day standard deviation (moving window) of daily movements to 180 days after release. Solid grey line represents the standard deviation of stable movements identified in A. Dashed lines represent threshold to acclimation (±75% grey line value).

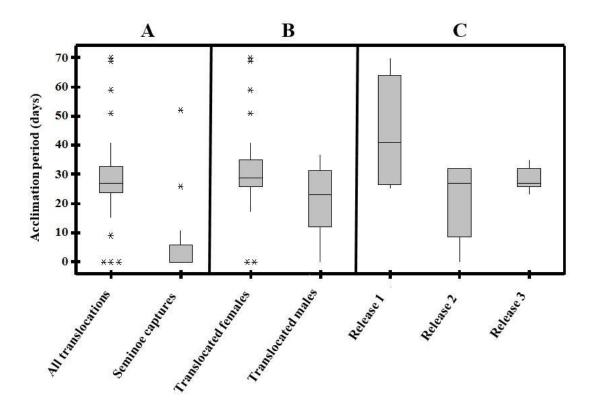


Figure 2.3. Box plot depicting acclimation periods of differing cohorts of low-elevation, non-migratory bighorn sheep via translocation and capture-and-release efforts from 2009 to 2011 in the Seminoe Mountains, Wyoming, USA. (A) All bighorn cohorts; (B) females and males; and (C) females from 3 release efforts. Box plots include the interquartile range (25th-75th percentile) in days to acclimation; horizontal lines inside boxes represent median days to acclimation; lower and upper whiskers are 1.5 times the interquartile range; asterisks above and below whiskers are outliers in days to acclimation.

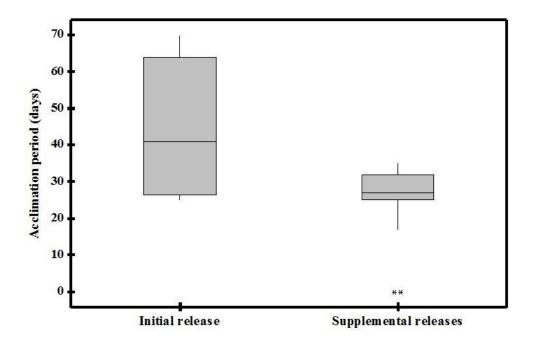


Figure 2.4. Box plot depicting a decrease in acclimation period of translocated female bighorn sheep in supplemental releases, versus initial translocation release effort, to the Seminoe Mountains, Wyoming, USA, in 2009 and 2010. Box plots include the interquartile range (25th-75th percentile) in days to acclimation; horizontal lines inside boxes represent median days to acclimation; lower and upper whiskers are 1.5 times the interquartile range; asterisks above and below whiskers are outliers in days to acclimation.

CHAPTER 3

AN EVALUATION OF DISTRIBUTIONAL SHIFTS IN PAIRED HOME RANGE ESTIMATES

In the format for manuscripts submitted to the *Journal of Mammalogy*

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Key words: Bighorn sheep, Brownian bridge, GPS, home range comparisons, *Ovis canadensis*, utilization distribution, Wyoming

A variety of methods are commonly used to quantify animal home ranges using location data acquired with telemetry. High-volume location data acquired from global positioning system (GPS) technology provides researchers the opportunity to identify various intensities of use within home ranges, typically quantified through utilization distributions (UD). However, the wide range of variability evident within UDs constructed with modern home range estimators is often overlooked or ignored during home range comparisons, and challenges may arise when summarizing distributional shifts among multiple UDs. We describe a simple approach to gain additional insight to home range alterations by comparing UDs across the full spectrum of distributions and summarizing comparisons into meaningful results. We demonstrate the efficacy of this approach using GPS location data from 16 bighorn sheep (*Ovis canadensis*) to identify distributional changes before and after habitat alterations, and discuss advantages in its

application during distributional comparisons in home range size, overlap, and joint-space use. We identified both stable and decreasing trends in various UD comparisons, driven by a potential combination of biologically meaningful space use of the animal and restricting data when comparing core home range areas. Overall, our results highlight the importance of conducting multi-scale assessments when comparing distributions. We encourage researchers to expand comparative home range analyses to gain a more comprehensive evaluation of distributional changes, and to evaluate comparisons across a spectrum of home range levels.

Location data are often used to estimate animal space use that delineates the predicted area of occurrence for individuals or groups of animals, and are often used to identify key resources within the boundaries of predicted occurrences. Traditional methods of estimating home ranges are as simple as a minimum convex polygon (MCP), where peripheral animal locations are connected to create a single polygon with no concave elements (Blair 1940; Mohr 1947). Modern global positioning system (GPS) technologies increase the ability to gather and store voluminous location data with high accuracy in comparison to very high frequency (VHF) systems (Moorcroft 2012; Tomkiewicz et al. 2010; Walter et al. 2011). Accordingly, home range estimators have evolved to quantify home ranges using high-volume GPS data, and often provide estimates of the intensity of use within the extent of the home range, commonly represented through a cell-based output known as a utilization distribution (UD; Van Winkle 1975; Worton 1989). Animals rarely utilize the area within a home range extent in a uniform pattern, but rather select areas based on habitat requirements, thus exhibiting non-random movements within the home range (Burt 1943). Accordingly, UDs provide information about the spatial extent of the

animal home range as well as a measure of the spatial intensity of use, where core use areas are defined as portions of the home range that exceed equal-use patterns (Samuel et al. 1985).

Comparisons among home ranges, particularly contrasting the extent of home ranges, are often conducted at chosen home range proportions of the volume of 3-dimensional utilization distributions, or isopleths, which can be used to determine core ranges (Börger 2006). These isopleths are typically defined at 50% [core home range] and 95% [total home range extent] levels (e.g., Garitano-Zavala et al. 2013; Heupel et al. 2004; Kie et al. 2010; Ostfeld 1986) for individual animals, or for all marked animals in a sample to gain population inference (Fieberg and Börger 2012). However, applying a home range estimator that quantifies intensity of use through a UD allows visual inspection across all proportional levels of the home range. It may be seen, then, that two-dimensional comparisons conducted at chosen home range isopleths may overlook or exclude variability in the intensity of use across the entirety of the home range that is provided by the UD (Kernohan et al. 2001; Kie et al. 2010; Millspaugh et al. 2004). Conceptual examples of these ideas are provided in Fig. 3.1. These exaggerated examples show obvious differences in intensity of use and potential misrepresentations of home range sizes at 50% and 95% isopleths, but empirical high-volume GPS data used to generate UDs often result in complex distributions with disconnected polygons that make accurate interpretation difficult.

A suite of metrics have been developed to compare two and three-dimensional home range representations, dependent on the ecological question associated with the analysis (Table 3.1). Fieberg and Kochanny (2005) provide detailed discussion on the use and efficacy of many of these comparative metrics. If individual animals are used as the experimental unit for comparisons, challenges arise on how to quantify and summarize population-level estimates while incorporating individual variability, regardless of the metric used for comparisons. In other

words, it is relatively simple to overlap individual UD pairs to visually inspect and identify distributional changes, but it becomes increasingly difficult to compile and summarize multiple comparisons to gain population-level inference without losing detail within each experimental unit. Researchers encourage the use of the individual as the experimental unit, especially within resource selection studies (Thomas and Taylor 2006), and sampling multiple individuals is an effective method to gain population-level inference of space use (Powell and Mitchell 2012).

We expand the application of a modern home range estimator and well-established UD comparative measures to comprehensively evaluate distributional shifts across home range levels, and to summarize individual comparisons to gain population-level inference on changes in home range size, overlap, and similarity in animal space use. Researchers should find utility in expanding comparative home range analyses to gain a more comprehensive evaluation of distributional shifts. In particular, we demonstrate opportunities to assess trends in comparisons across a spectrum of home range levels, better describing changes in animal space use.

MATERIALS AND METHODS

Example data.—As an application example, we describe the process we implemented to compare distributions of 16 bighorn sheep (*Ovis canadensis*) using paired GPS data collected before (2009–2011) and after (2011–2013) fire-mediated habitat alterations. GPS transmitters attached to these bighorns collected location data prior to the initiation of fires that occurred in early May 2011 (pre-fire), and subsequent recaptures of these animals continued data collection through June 2013 (post-fire). We used the "BBMM" package (Nielson et al. 2013) in the R statistical environment (R Development Core Team 2012) to create a pair of UDs to be compared for each bighorn (i.e., our experimental units). Brownian Bridge Movement Models (BBMMs) have gained in popularity due to incorporation of estimated animal motion variance,

GPS error, and the time and distance between successive locations to provide a cell based output that estimates probability of occurrence across a landscape (Bullard 1999; Horne et al. 2007). Because of dependence on sequential, autocorrelated location data, BBMM home range estimators are quantified on an individual basis, and the ever-increasing volume and detail of GPS data that challenge less-modern home range estimators (Kie et al. 2010) are often utilized within BBMMs to estimate home ranges and map migration paths using fine-scale location data. Although not unique to the BBMM estimator, individual home range estimates allow the use of each animal as an experimental unit, alleviating the risk of individuals with high volume locations influencing distribution at a population level when pooling location data and using a density estimator. Overall, an array of home range estimators can provide quality UD representation. While we do not advocate for any specific estimator, we found the BBMM estimator applied well to our specific dataset.

Estimator standardization.—When conducting home range comparisons, it is important to minimize error by standardizing sampling regimes and parameters of the chosen home range estimator (Fieberg and Börger 2012). Accordingly, within a BBMM characterized by uniform distances between locations, as the temporal duration between consecutive locations increases, the probability of random movement away from the direct path between sequential locations also increases. This increase in animal motion variance results in an expansion of the resulting utilization distribution (Horne et al 2007). Because some GPS collars were programmed to collect location data every hour, we standardized GPS data by selecting every fifth location from 1-hour fix rates to match 5-hour location data collected from recaptured animals. The resulting 5-hour fix rate was used to ensure animal motion variance was calculated using consistent fix rates among all paired individual datasets. GPS fix-rate success was high for animals in our sample

(mean > 90%); even so, we set parameters of the home range estimator to censor bridges with an associated time lag exceeding 305 min to ensure models did not inflate estimated space use if intervals exceeded 5 hours. We also censored initial location data from captured individuals by removing locations associated with sporadic animal movements following releases to allow for adequate temporal acclimation after releases (Clapp et al. 2014).

We set parameters of the home range estimator function to define a consistent spatial extent for each paired dataset that encompassed all animal locations for both pre-fire and postfire durations. We set a 30 m x 30 m cell size output to overlap paired BBMM utilization distributions and to subsequently conduct effective cell-by-cell calculations. Because the Brownian bridge estimator is based on a Gaussian distribution where the probability of occurrence infinitely approaches zero, we rounded probabilities to machine precision to define contours of each home range estimate (cell values less than 1 e⁻¹⁵ rounded to zero; Fieberg and Kochanny 2005). Because GPS data acquired from some individuals were less than a full calendar year in duration, we standardized each pair of model outputs using only data collected during identical timeframes, by ordinal date, for each pair of home range estimates. For example, if a pre-fire UD was estimated using location data collected only from 1 June through 15 December, we restricted the corresponding post-fire UD to incorporate only location data collected during the same period. Although the distribution of some animals may be dependent on season, sex, and in relation to habitat components, we used the standardization of least common timeframe where adequate paired data were gathered to estimate overall annual home range differences.

Utilization distribution comparisons.—We used the bbmm.contour function (package BBMM) to identify proportional contour levels for each UD ranging from 99% (most inclusive

home range estimate) to 5% (highest core use areas) in 5% intervals (Fig. 3.2). We stored the relative probability threshold values that represented each contour level for each UD. We then overlaid each pair of utilization distributions for visual inspection (Fig. 3.3).

It is advantageous to apply multiple metrics and methods when analyzing and comparing home range data (Fieberg and Börger 2012). Therefore, we calculated comparative measures (Table 3.1), and reported a chosen subset that best assessed distributional changes for bighorn sheep in relation to 1) changes in home range size, 2) proportion of home range overlap, and 3) similarity between UDs. Similarity between paired utilization distributions were reported using two indexes. The utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) incorporates both the similarity in joint-space use and the area of overlap between distributions, and many studies have used the UDOI index to estimate joint-space use (e.g., Berger and Gese 2007; Pauli and Peery 2012; Thiebot et al. 2012). Fieberg and Kochanny (2005) found that while UDOI may best estimate the degree for which two animals share the same space, Bhattacharyya's affinity (BA; Bhattacharyya 1943) may be more appropriate to compare overall similarity between utilization distributions; therefore, we reported both indices to compare distributions. Volume of intersection (VI) is another commonly used index that calculates the cumulative minimum volume of intersection shared among distributions. This comparative statistic was considered but was not reported due to similarity between VI and BA trends as well as documented high correlation between these comparative statistics (Kochanny et al. 2008).

Because variation in probability of use, home range size, overlap, and similarity depend largely on the chosen contour of the UD that was examined, we summarized data based on multiple contour levels of the home ranges. We quantified comparative metrics, starting with the most inclusive home range contour (99% isopleth) for each experimental unit. After calculating

metrics at the broadest home range level, we used the appropriate probability threshold values to reclassify both pre-fire and post-fire UD rasters at the next sequential contour level (95% isopleth). We used a conditional statement to set cell values less than the 95% contour threshold to zero (see Fieberg and Kochanny 2005). Because the remaining cell values must sum to one to remain a relative utilization distribution, we reclassified the remaining cells by dividing each cell value by the sum of the remaining cell values within the UD (Fig. 3.4). We then recalculated comparative metrics at this level.

We repeated this process at each home range level in ~5% intervals until we reached the highest defined intensity of use for the original UDs (5% isopleth). We summarized these comparisons for all individuals to quantify population-level distributional shifts across home range levels. We report trend data as mean and 95% point-wise confidence intervals using a *t*-distribution for each comparative metric or similarity index. We conducted statistical analyses and data management in R 2.15.3 (R Development Core Team 2012).

RESULTS

Variation was evident among individual bighorn UD comparisons (Fig 3.5), giving additional insight to how individuals included in the sample may influence mean distributional changes. When summarizing comparative measures to gain population-level inference, results from our example showed an approximate 200% increase in home range size consistently from the full home range extent to the highest intensity of use or core range areas (Fig. 3.6A). Because the difference in relative home range size was quantified by dividing post-fire by pre-fire area, a metric equal to one indicated no relative change in home range size (Fig. 3.6A). When comparing how much post-fire home range overlapped pre-fire distributions, at the full extent, home ranges averaged 50% overlap with paired home ranges before the initiation of burns. This

trend decreased to ~25% overlap at extreme core range levels (Fig. 3.6B). When examining similarity between UDs, we identified a sharp decrease in estimated joint-space use (UDOI) ranging from the 99% home range until an apparent "threshold" was reached at approximately the 70% isopleth after which the decline slowed as UDOI moved toward an asymptote (Fig. 3.6C). Using the BA index, we found mean similarity in distributions exhibited a linear decrease at increasing core range contours (Fig. 3.6D).

In summary, results from our example indicated that bighorns within our study area uniformly expanded post-fire home range area across isopleth levels, with increasing space use after fire exhibited at the expense of lower intensity of use within pre-fire core areas. While insightful to overall space use, this change in home range size gave little indication of potential changes in the spatial arrangement of distributions across the landscape. However, when examining home range overlap, bighorns also exhibited a change in the relative proportion of post-fire distribution that overlapped the corresponding pre-fire distribution in a decreasing trend from approximately 50% to 25% at increasing core range isopleths (Fig. 3.6B). This relative proportion of overlap was likely influenced by the increase in home range size, with much prefire distribution within the extent of post-fire areas. Notwithstanding, it rendered a relative expansion that increased proportionally across increasing core area levels (Fig 3.6B). The change in UDOI values that dropped precipitously from the 99% contour concurred with what was shown in overlap (Fig. 3.6C) because UDOI was calculated using joint-space use as well as area of overlap between UDs (which showed relatively high overlap at more inclusive home range proportions; Fig. 3.6B). The BA index also showed a decrease in UD similarity at increasing core range isopleths, indicating that core home ranges were altered to a higher degree than full home range extents (Fig. 3.6D).

DISCUSSION

We investigated a simple approach to assess changes in paired utilization distributions, and found notable benefits from conducting UD comparisons individually and across a spectrum of home range levels. By conducting paired comparisons using the individual animal as the experimental unit, outliers and individual variation were easily identified, which otherwise may have gone unnoticed if we pooled or averaged distributions across animals (Fig. 3.5). Also, instances where individuals completely realigned home ranges were apparent in overlap and similarity analyses, and by identifying these animals we found mean comparisons typically shifted to lower values, but rendered the trend across home range levels unchanged.

The trend in comparative measures we identified across home range levels suggest broader questions about properly estimating the extent of home ranges. Home range extents are often chosen at a contour that encompasses a selected percentage of total space used (Anderson 1982), but appropriate levels may be difficult to quantify. Similarly, Fieberg and Börger (2012) found it unfortunate that most studies used *ad hoc* definitions to delineate core areas (e.g., 50% isopleth) without first considering biologically meaningful research questions and subsequently choosing commensurate analysis methods. Specifically, the size and location of core home ranges may depend on the method used to determine home range size, and substantial influences on core areas may result based on the estimated home range boundary and underlying distribution (Samuel et al. 1985). Although conducting and summarizing comparisons across a spectrum of home range levels did not allow us to identify specific isopleth values that best identified core areas, we gained insight into how home range comparisons changed across levels.

Ecologists are commonly faced with decisions regarding scale, and studies often report the use of multi-scale approaches for replete assessments, depending on associated ecological questions (e.g., Börger 2006; Boyce 2006; DeCesare et al. 2012; Millspaugh et al. 2004). By comparing home range estimates across levels, we identified thresholds in isopleth values that resulted in marked differences in home range estimates. For example, we found that mean UDOI values showed overlap (95% confidence intervals) from the 99% home range level to the 85% level, but lower isopleth levels were significantly different from this range (Fig. 3.6C). These results revealed how differences in similarity can change throughout the spectrum of isopleth levels—not necessarily occurring at only 95% and 50% levels. In our example, the UDOI index may indicate that isopleths greater than ~70% may not be as favorable for similarity comparisons as those less than 70%, where a downward trend existed, but toward an asymptote that may better represent an estimate of overall similarity. Also, core home range comparisons may potentially be influenced by restricting input that reduces the likelihood of high similarity among UDs near the peak of distributional surfaces—resulting in a typical decline in similarity measures. Although not available in our dataset, a control group (bighorns not affected by habitat alterations) would be beneficial to further investigate these influences. However, similarity can theoretically remain high at core home range levels if animals shift the extent of their distributions while sustaining uniform core area use. If desired, the ability to conduct comparative tests (e.g., paired t-test) between chosen isopleths remained. However, statistical tests are often intended to answer a specific question regarding distributional changes (e.g., "did home range area increase?") with a definitive "yes" or "no" answer dependent on a chosen alpha value, sample size, and sample variation. We argue that given the uncertainty in extent (influenced by a chosen home range estimator) coupled with the difficulty in accurately identifying core area isopleths, assessing the trend in comparisons across isopleths better revealed not only if distributions changed, but provided insight regarding how these changes occurred. It was also apparent that while conducting home range comparisons, as the home range contour decreased to include only core

areas of use, the potential to overlook seldom used but vital areas of the home range, such as movement corridors or migration patterns, may increase. Regardless of the chosen home range estimator or comparisons at any specific home range level, it was the ability to assess trends in which we found the most insight in our analysis, were we "filled the gaps" often overlooked if only comparing predetermined home range contours.

When comparing across home range contours, we understand contours are not independent of each other, meaning larger home range extents influence core home range levels. This is to be expected given that comparisons are conducted among utilization distributions that are inherently reliant on correlation. Therefore, we did not consider correlation among home range levels limiting the analysis, but that correlation across comparisons mimics correlation evident in the distributions themselves. For example, when examining a 3-dimensional utilization distribution alone, we consider the ability to identify areas of increased space use a benefit, though these areas are certainly dependent upon lower levels of the distribution. In similar fashion, comparisons across isopleths inherit the correlation of the distributions, as well as the benefit to identify how distributional changes are rendered throughout. When summarizing comparisons, it is evident that all home range estimators are subject to associated error when estimating space use, some of which may be difficult to account for when averaging across animals to gain population-level inference. However, when one considers the home range estimator and comparative values as consistent measurements applied to each experimental unit, one may identify the average change in measurements among UDs to describe population-level changes in space use.

Limitations may exist when reclassifying UDs to conduct multi-level home range comparisons. Each reclassification decreases the number of cells within the restricted home

range level, and this change could influence the results of the comparative measures. Therefore, an appropriate resolution (cell size) should be identified prior to conducting home range comparisons. For example, a tradeoff develops when calculating cell-based UDs at high resolution (e.g., 1 m x 1 m) using complex home range estimators such as the BBMM. These are computationally challenging for many systems, and require extensive time to calculate, even at fast processing speeds. However, at coarse resolutions (e.g. 100 m x 100 m) the accuracy of comparative measures, particularly at highly concentrated contour levels (e.g., 5% core home range may encompass a small area), may not yield desired accuracy. Overall, the method we used compared UDs at differing home range levels, but did not change the resolution of the cell size as home range contour restrictions occurred. It also should be noted that other methods to calculate comparative metrics exist, especially tailored for comparing independent distributions. The "adehabitat" package (Calenge 2006) in the R statistical environment (R Development Core Team 2012) is often used to conduct comparisons based on a kernel density UD at a desired contour. This method provides a matrix output that shows UD comparisons among multiple animal or population UDs. However, we found it advantageous to reclassify and compare space use repeatedly for the same animal at multiple contours when comparing paired distributions, allowing a more comprehensive evaluation of distributional changes.

In conclusion, we compared temporal distributions using paired data from the same animals before and after habitat alterations, but other useful applications may include comparing diurnal and nocturnal animal movement patterns, comparing seasonal migrations patterns, or identifying changes in distributions due to anthropogenic disturbances. We found a more comprehensive evaluation of distributional changes can be identified using well-established techniques readily available to researchers—done by simply applying these techniques across a

spectrum of home range scales and summarizing data to identify trends in distributional response. The benefit of the utilization distribution is that it represents spatial variation in intensity of use for the entire home range. Our analysis allowed comparative metrics to be represented and interpreted in similar fashion across all home range levels, providing an in-depth evaluation of changes in animal space use.

ACKNOWLEDGMENTS

We thank S. E. Albeke, C. B. Buchanan, M. E. Dillon, T. L. McDonald, K. T. Smith, and L. A. Varelas for support in data management and analysis techniques. G. S. Hiatt and B. A. Brinegar, Wyoming Game and Fish Department, provided logistical and field support. We thank France Flying Service and Sky Aviation, as well as local landowners for study area access. The University of Wyoming, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and Wyoming Wild Sheep Foundation provided funding. H. Sawyer provided helpful comments to an earlier draft of our manuscript.

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TABLE 3.1.—Common metrics used to compare home range estimates (see Fieberg and Kochanny 2005). Within the equations, A_x represents the area of the respective home range, and $A_{1,2}$ represents the area of overlap between home ranges.

Comparative metric	Explanation	Typical representation	Equation
Size	Relative change in home range size	2D	A_2/A_1
Overlap	Proportion of HR overlap (directional)	2D	$A_{1,2}/A_x$
Volume of intersection (VI)	Minimum joint-space use between UDs	3D	$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min \left[\widehat{\text{UD}}_{1}(x, y), \widehat{\text{UD}}_{2}(x, y) \right] dx dy$
Bhattacharyya's affinity (BA)	Product-based UD similarity index	3D	$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{\widehat{\mathrm{UD}}_{1}(x,y)} \times \sqrt{\widehat{\mathrm{UD}}_{2}(x,y)} \ dxdy$
Hellinger's distance (HD)	Index of relative distance between UDs	3D	$HD = 2 \times (1 - BA)$
Utilization distribution overlap index (UDOI)	Product-based index of degree of joint-space use	3D	$A_{1,2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \widehat{\text{UD}}_{1}(x,y) \times \widehat{\text{UD}}_{2}(x,y) dx dy$

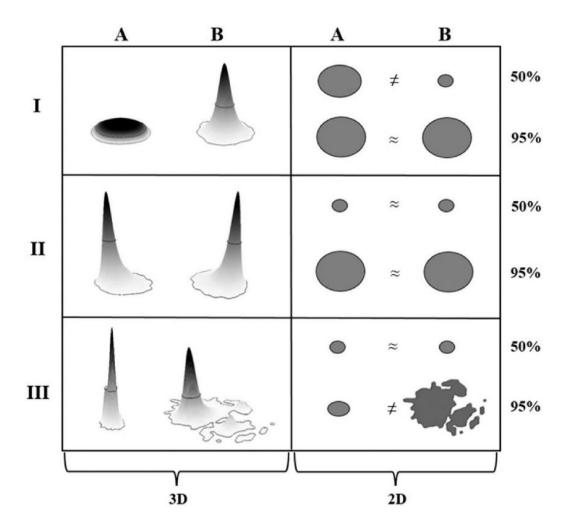


FIG. 3.1.—Conceptual examples of paired home range comparisons at 50% and 95% isopleth values in 2-dimensional and 3-dimensional aspects. (A) and (B) represent the UDs being compared in each scenario. (I) Comparison between full home range estimates (95%) indicate little difference in home range size, but on closer inspection of the UD, the intensity of use shows a marked change in core area use (50%). (II) A scenario where the full extent and core home range sizes are nearly identical, but the intensity of use has shifted spatially within. (III) Extent of 95% home range indicates a marked expansion in space use, but on closer inspection of the UD, the majority of 50% core use area remains basically unchanged.

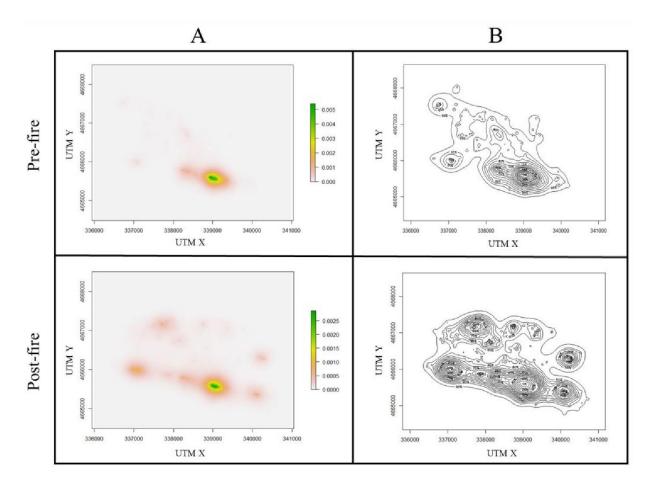


FIG. 3.2.—Brownian bridge utilization distribution rasters (A) and associated contour lines (B) before (2009–2011) and after (2011–2013) fire-mediated habitat alterations for an individual female bighorn in the Seminoe Mountains, WY, USA.

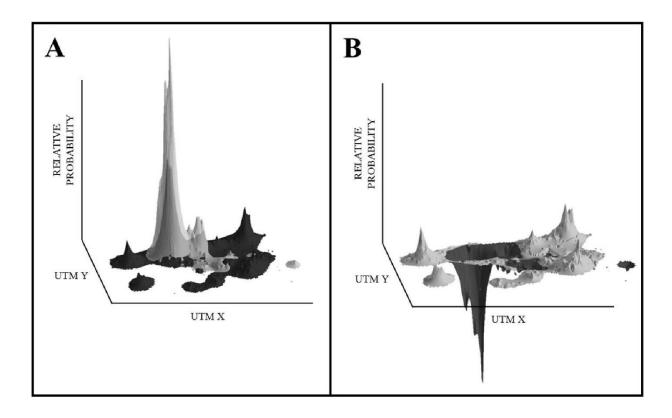


FIG. 3.3.—3-dimensional representation of a female bighorn UD surface overlay in the Seminoe Mountains, WY, USA. (A) Overlay of surfaces pre-fire (2009–2011; light) and post-fire (2011–2013; dark). Note that due to the relative probability of occurrence, post-fire distribution expanded at the expense of a decrease in pre-fire core area use (light and dark overlap). (B) UD surface showing difference in probability of occurrence after fires. Areas that increased in use after fires are positive and shown light, whereas areas that decreased in use are represented as dark shaded depressions (i.e., negative).

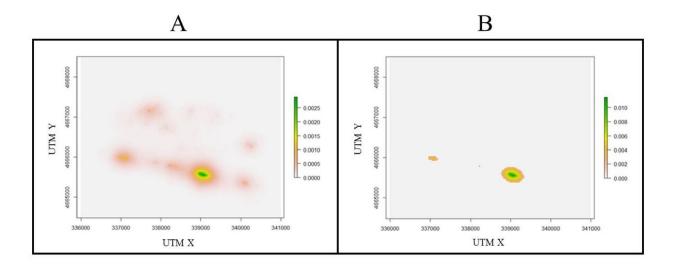


FIG. 3.4.—Example of post-fire utilization distribution raster at a 99% contour level (A), and reclassified at a 25% contour level (B) for a female bighorn in the Seminoe Mountains, WY, USA.

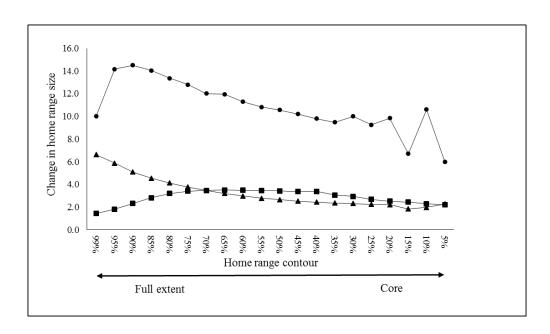


FIG. 3.5.— Individual variability in the relative change in home range size for 3 female bighorns across increasing home range contours before (2009–2011) and after (2011–2013) fire-mediated habitat alterations in the Seminoe Mountains, Wyoming USA. Relative change in home range size was computed as A_2/A_1 . Because the difference in relative home range size was quantified by dividing post-fire (A_2) by pre-fire area (A_1), a metric equal to one indicates no relative change in home range size. Note the variability among individuals including an outlier showing highly variable and increased home range size (circle markers), while others show decreasing (triangle) or increasing (squares) trends – particularly at larger home range extents.

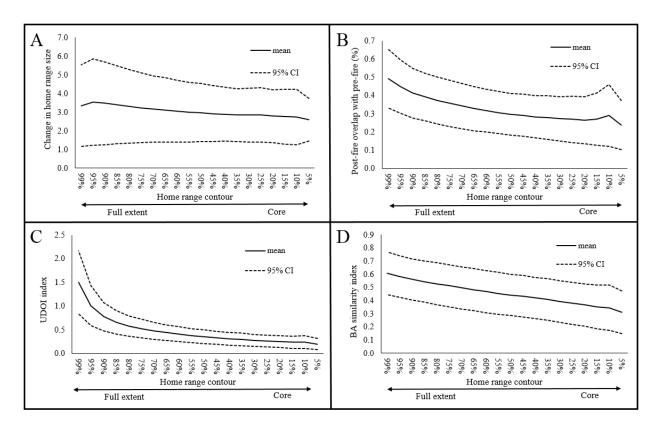


FIG. 3.6.—Distributional comparisons of 16 bighorn sheep across increasing home range contours before (2009–2011) and after (2011–2013) fire-mediated habitat alterations in the Seminoe Mountains, Wyoming USA. (A) Average relative change in home range size. Relative change in home range size was computed as A_2/A_1 . Because the difference in relative home range size was quantified by dividing post-fire (A₂) by pre-fire area (A₁), a metric equal to one indicates no relative change in home range size. (B) Mean proportion of post-fire home ranges that overlapped pre-fire distributions. Proportion of post-fire home range overlap was computed as $A_{1,2}/A_2$, where A_2 represents the area of the post-fire home range, and $A_{1,2}$ represents the area of overlap between home ranges. (C) Mean similarity calculated with utilization distribution overlap index (UDOI) between pre-fire and post-fire showing degree of joint-space use. UDOI was computed as $A_{1,2} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} U \overline{D}_1(x,y) \times U \overline{D}_2(x,y) \, dx dy$. Typical UDOI values range from 0–2, but can exceed these norms by varying degrees of overlap. (D) Bhattacharyya's affinity

index (BA) showing overall similarity between distributions. BA values scale from 0–1, and were computed as $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{U \widehat{D}_1(x,y)} \times \sqrt{U \widehat{D}_2(x,y)} \, dx dy$.

CHAPTER 4

PROVISIONAL IMPACTS OF FIRE-MEDIATED HABITAT ALTERATIONS ON AN ISOLATED UNGULATE POPULATION

In the format for manuscripts submitted to the Journal of Wildlife Management

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ABSTRACT Translocation is considered a primary tool used to reestablish or bolster waning populations of many wildlife species, and is often accompanied by habitat alterations in an effort to improve and expand suitable habitats. We used global positioning system (GPS) locations collected from bighorn sheep (*Ovis canadensis*) translocated to the Seminoe Mountains, Wyoming, USA in 2009 and 2010, as well as from bighorns captured and released in our study area in 2011, to investigate provisional impacts of prescribed and wildfire-mediated habitat alterations in 2011–2012. We conducted analyses that quantified home range distributional changes, resource selection, and survival of bighorn sheep. Bighorns expanded home range distributions after fire events by ~200%, and shifted core home range areas to a higher degree than home range extents. Resource selection (RSF) model coefficients suggested no resource selection for fire-treated areas, although independent proportional use increased in areas treated with prescribed burning. Bighorn survival decreased after burns in 2012 that were accompanied by severe drought conditions, with ~30% mortality recorded from radio-collared animals.

Evidence suggested prescribed burns conducted under favorable conditions (2011) induced potentially positive bighorn responses including high survival and increased use of treated areas, whereas fires that occurred during drought conditions that were generally more severe and widespread (2012) coincided with increased bighorn mortality rates through 2013. Although managers often have limited control over naturally-occurring fires, our study suggests that large-scale fires coupled with unfavorable climate conditions can render bighorns unable to access adequate forage to meet nutritional requirements, because sheep are unwilling to forego site fidelity. Because provisional impacts of fire-mediated habitat alterations on bighorn populations are highly dependent on ensuing vegetative recovery, consideration should be given to the timing, extent, and spatial coverage of prescribed burns. We recommend prescribed burns should not fully encompass current bighorn distributions, and that other methods of habitat improvement be considered when applicable.

KEY WORDS bighorn sheep, global positioning system, *Ovis Canadensis*, prescribed burn, resource selection, survival, translocation, utilization distribution, wildfire, Wyoming.

Translocation is a primary tool used to reestablish or bolster waning populations of many wildlife species, and is often accompanied by habitat alterations in an effort to improve and expand suitable habitats (Osborne and Seddon 2012). While direct habitat evaluations are often conducted after alterations occur, assessment of wildlife responses to treatments provide key information on how habitat treatments impact translocated animals. To identify impacts to resident populations, distributional response may be assessed, often measured by changes in animal space use and habitat selection. However, distributional responses can be limiting if not

assessed in concert with demographic response of the target population to identify not only if habitat alterations result in selection for treated areas or expanded space use, but actually improve the overall fitness and productivity of the population. Bighorn sheep (*Ovis canadensis*) populations in western North America dramatically declined throughout their range in the early 20^{th} century, with multiple populations extirpated from historical habitats. A primary obstacle in bighorn sheep restoration is that bighorn are poor colonizers (MacArthur and Wilson 1967), and are known to exhibit strong site fidelity to their home ranges after identifying escape terrain, water sources, and lambing habitat (Geist 1970, 1971, Shackelton et al. 1999). Because they do not readily search for unoccupied habitat, numerous translocation efforts have been undertaken to restore bighorn populations to historical habitat and augment waning populations (Hansen 1980). By 1990, over 50% of all bighorn populations originated from translocation efforts (Bailey 1990), making translocation a key component to bighorn restoration.

Habitat analysis and evaluation play a key role in the success of translocated ungulate populations (e.g., Beck et al. 2006). These evaluations should be extensive because translocations of large animals are known to be time consuming, expensive, and logistically and politically challenging (Beck et al. 1994, Biggins and Thorne 1994, Wolf et al. 1996, Dunham 1997, Fritts et al. 1997). For example, reported costs for the translocation of each bighorn sheep in the United States was \$2,257 in 1990 (Bleich 1990*a*). Increased costs due to inflation raised this estimate to over \$3,000 per animal by 1999 (Zeigenfuss et al. 2000), and over \$4,000 by 2013 (BLS 2013).

Modified habitat suitability models for the Rocky Mountains suggest reintroducing bighorn into large patches of suitable habitat that promote movements and migrations to increase the success rate of translocations (Singer et al. 2000). Many bighorn sheep populations migrate

through extensive elevational gradients; however, long-distance migrations do not occur among isolated or non-migratory bighorn populations restricted by suitable habitat. For instance, some successful desert bighorn (*O. c. nelsoni*) populations use seasonal ranges separated by as little as 2–30 km annually (Ough and deVos 1986, Bleich et al. 1990*b*). Bighorn sheep concentrated to a restricted habitat, especially on winter range, may be more susceptible to disease, increased predation, limited genetic connectivity, and higher use of available forage (Risenhoover et al. 1988). Thus, it has been recommended to translocate bighorn sheep to large areas that may support multiple subpopulations, and eliminating tall vegetation through burning or easements to release restrictive habitats and encourage the use of movement corridors (Smith et al. 1999, Singer et al. 2000).

Past studies have documented variable increases in forage nutritional quality and production in various habitats following burning for up to 7 years (DeWitt and Derby 1955, Christiansen 1973, Merrill et al. 1980, Boerner 1982, Seip and Bunnell 1985, Cook et al. 1994, Sachro et al. 2005, Van Dyke and Darragh 2007). Consequently, prescribed burning is often used as a management tool to benefit bighorn sheep and has been shown in many cases to improve diet quality and foraging efficiency (Hobbs and Spowart 1984, McWhirter et al. 1992). In addition to potential nutritional benefits of fire, open habitat created by fire may establish movement corridors that encourage dispersal to other available habitats (Risenhoover et al. 1988). While these studies have examined changes in vegetation in burned and unburned areas, a deficiency persists in determining the effects of fire on bighorn sheep demography. Greene (2010) conceded that much of the evidence linking forage to demography is derived from artificial experimental systems, anecdotal, theoretical, or lacks replication, highlighting the need to further investigate *in situ* demographic response of bighorns due to impacts from fire.

Our study aimed to quantify provisional impacts of fire-mediated habitat alterations to a recently translocated bighorn population in the Seminoe Mountains, located in south-central Wyoming, USA. We collected GPS location data from radio-collared bighorn sheep in the Seminoe Mountains from 2009–2013 that included 3 bighorn translocation events as well as a capture event within the study area after the initiation of prescribed burning. Our specific objectives were to 1) identify changes in bighorn distribution, 2) investigate potential habitat selection for treated areas, and 3) quantify and compare demographic response of bighorn sheep before and after fire events. We predicted bighorn sheep would both expand distribution and select for treated habitat after fires in response to a combination of increased forage quality within treated areas and expanding shrubby and forested habitat previously restricting bighorns by visual barriers. Concomitant analyses included estimating survival of bighorn sheep and quantifying survival of marked animals under various responses to fire-mediated habitat alterations, where we predicted increased survival rates commensurate with favorable habitat improvements.

STUDY AREA

The Seminoe Mountains (106°56′0.000″W, 42°10′0.000″N) are located approximately 40 km north of Sinclair, Carbon County, Wyoming, USA (Fig. 4.1). They lie on a latitudinal orientation with prominent south and north faces, with the 16.7 km² Wyoming Game and Fish Department's (WGFD) Morgan Creek Wildlife Habitat Management Area (WHMA) positioned in the center of the mountain range (Fig. 4.1). Topography (elevation range: 1830–2500 m) in the study area (~85 km²) ranged from long draws and ridges in the western portion, to near vertical cliffs where the North Platte River flows northerly through the range. Land status included 80% federal, 10% state, and 10% private lands. Primary vegetative cover types included sagebrush (*Artemisia*

spp.), grassland, and conifer with a mixed shrub understory intermixed with mountain shrub, riparian meadow, and riparian broadleaf cover types. Dominant coniferous trees included limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*P. ponderosa*), and Rocky Mountain juniper (*Juniperus scopulorum*), and deciduous tree species included aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), and narrowleaf cottonwood (*Populus angustifolia*). Shrub species included antelope bitterbrush (*Purshia tridentata*), big sagebrush (*A. tridentata*), and true mountain mahogany (*Cercocarpus montanus*). Hiatt (1997) provided lists of common grass and forb species for the study area. The 30-yr (1981–2010) average annual precipitation was 36 cm, with most precipitation occurring in spring. The 30-yr (1981–2010) average annual temperature was 7°C, resulting in 70–90 frost-free days, with 45% of annual precipitation falling as snow (Western Regional Climate Center 2013). High winds were common in the Seminoe area, especially on exposed slopes and ridges.

METHODS

Capture of bighorn sheep and habitat alterations

From December 2009 to December 2010, 52 bighorn sheep (40 F, 12 M) from 3 captures were translocated to the Seminoe Mountains in south-central Wyoming, USA from 2 sites in eastern Oregon and a single site in north-central Wyoming. Helicopter net-gunning was used to capture all bighorns, which were processed, marked, and translocated following state agency (Oregon Department of Fish and Wildlife, see Foster [2005]; WGFD, Chapter 10-1535 and Chapter 33-750 permits) approved protocols. Bighorns were restrained using front and rear leg hobbles and blindfolded to minimize stress during processing. Biological samples were taken from each captured bighorn for disease and parasite screening, and each animal underwent a physical examination by trained animal handlers or a state veterinarian that included documentation of

age, sex, and physical abnormalities. Animals were marked using self-piercing metal or plastic ear tags unless previous ear tags were evident, and 40 store-on-board GPS collars (13 Telonics, Inc., Mesa, AZ, GEN III, model TGW3500 collars and 27 Advanced Telemetry Systems, Isanti, MN, model G2110D) were affixed to 31 F and 9 M bighorn sheep. To accommodate different analyses using GPS data collected from bighorns, these collars had differing fix rates, with 22 collars configured to upload 1 GPS location every 1 hour for 6 months, and 18 to upload 1 GPS location every 5 hours for 18 months. GPS data were collected from translocated bighorns through spring 2011.

Prescribed burning initiated by the Rawlins Wyoming Field Office of the Bureau of Land Management (BLM) was conducted in spring 2011 and 2012 in the southern portion of the study area. Each spring, separate burns targeted dense shrub communities consisting of mountain mahogany and juniper and encroaching timber that may limit visibility and movement of bighorn sheep (Johnson and Swift 2000, Risenhoover et al. 1988). Spring ignitions resulted in mosaic burn patterns around snow cover and low fuel load areas, and totaled approximately 7.5 km². A wildfire also occurred within the study area in July 2012. This lightning-initiated wildfire burned approximately 12.6 km² of the northern portion of the study area. The combined area of these prescribed and natural fire-mediated habitat alterations resulted in approximately 20.1 km² or ~24% of burned habitat within the study area in 2011 and 2012 (Fig. 4.1).

On 2–3 December 2011, 20 F and 5 M bighorns were captured in the study area via helicopter net-gunning, processed, and released on-site throughout the study area following University of Wyoming Institutional Animal Care and Use Committee approved protocols (protocol 12012011) and WGFD Chapter 33-750 permit. Biological samples were taken from each captured bighorn for disease and parasite screening, and 25 refurbished GPS collars

(Telonics = 4, ATS = 21) were deployed on these bighorns to collect location data every 5 hours for 18 months until they remotely detached in June 2013. Captured bighorns that were previously collared and released in translocation efforts (n = 16) were identified, while metal ear tags were inserted into both ears of 5 bighorns born in the Seminoe Mountains that were never previously captured. Four bighorns captured in December 2011 were not fitted with GPS collars when translocated to the Seminoe Mountains.

Home Range Analysis and Distributional Alterations

We used 16 radio-collared bighorn sheep (12 F, 4 M) to isolate paired datasets to identify distributional changes of bighorn sheep after fires. We used the "BBMM" package (Nielson et al. 2013b) in the R statistical environment (R Development Core Team 2012) as a home range estimator to create a pair of Brownian bridge movement model (BBMM; Horne et al. 2007) utilization distributions (UD) for each bighorn sheep (i.e., our experimental units). We conducted home range comparisons following methods described in Chapter 3, and assessed home range alterations in relation to 1) changes in home range size, 2) proportion of home range overlap, and 3) proportion of home range overlap with fire-treatment areas. Because variation in probability of use, home range size, and overlap depend largely on the chosen contour of the UD that was examined, we summarized data based on multiple contour levels of the home ranges. We identified proportional contour levels for each UD ranging from 99% (most inclusive home range estimate) to 5% (highest core use areas) in 5% intervals, and stored the relative probability threshold values that represented each contour level for each UD. We compared home ranges, starting with the most inclusive home range contour (99% isopleth) for each experimental unit. We then used the appropriate probability threshold values to reclassify both pre-fire and post-fire UD rasters at the next sequential contour level, and recalculated comparisons at that level. We

repeated this process at each home range level in ~5% intervals until we reached the highest defined intensity of use for the original UDs. We summarized these comparisons for all individuals to quantify population-level distributional shifts across home range levels. We report trend data as mean and 95% point-wise confidence intervals for each comparative statistic or similarity index. We conducted home range analyses and data management in R 2.15.3 (R Development Core Team 2012).

Resource Selection Analyses

In our primary resource selection function (RSF) analysis, we used RSF modeling as a tool to identify female bighorn habitat selection for a specific predictor variable—selection of fire-altered habitats—while allowing other potentially important habitat components to compete as predictors in model selection and comparison of effect sizes. Comparing independently constructed RSF models before and after fires could result in different habitat variables contributing to best models, and would assume constant environmental and temporal impacts that may have occurred throughout the study period. Therefore, we constructed a single model from data gathered throughout the study period, and tested for significance of an interaction between pre-fire or post-fire location data (discrete binary predictor variable) and the distance to treated areas (continuous predictor variable).

We standardized location data gathered from each bighorn to include one GPS location every 5 hours (matching the maximum GPS fix-rate schedule), and censored initial movements to allow bighorns to acclimate after translocation or capture releases (Clapp et al. 2014).

Acquisition of GPS fixes was high in our study, averaging over 90% success rate for collared bighorns, which indicated no need to alter RSF analysis strategies to accommodate for potential bias associated with low GPS fix success (Nielson et al. 2009). Resource selection can be

identified when animals utilize a resource disproportionate to what is available on the landscape (Manly 2002, Hall et al. 1997). To delineate availability in our resource selection analysis, we merged 95% contours from BBMM home range estimates of each GPS-collared individual throughout the duration of the study period (Dec 2009–June 2013), eliminating likely non-suitable habitats. Because the purpose of the RSF was to specifically identify selection of treated habitat, we refined availability to areas within a 5 km buffer from the perimeter of treated areas, where habitat alterations had a higher likelihood of influencing bighorn habitat selection. This procedure eliminated areas occupied by individuals that dispersed or spent time away from the study area. We censored large bodies of water that fell within available areas, but because we documented bighorn movements across water bodies during summer and winter seasons, we assumed water did not constrain bighorn selection and included areas east and west of the North Platte River system as available.

To quantify RSF response, we generated circular sampling units with a radius of 150 m that were small enough to isolate and represent habitat components across the landscape (Millspaugh et al. 2006, Sawyer et al. 2006), but large enough to encompass adequate volume of locations to determine intensity of use and approximate error distributions (Sawyer et al. 2009a), and that exceeded the expected spatial error associated with GPS location acquisition (Nielson and Sawyer 2013a). We randomly distributed 2000 sampling units with replacement across the study area to ensure independence in the sampling unit response (Sawyer et al. 2006, 2009a), allowing sampling units to overlap and for location data to fall outside or within one or more independent sampling units. We then quantified intensity of use as the total number of locations within each sampling unit. Unlike typical RSF model interpretations that often include effect size plots and predictive maps, our RSF models were used as a tool to test a specific hypothesis

regarding identification of bighorn habitat selection for fire-treated areas. Because we did not use RSFs as predictive models, response variables were unaltered and left as count data during modeling. We used a negative binomial general linear model because count data exhibited over-dispersion from a Poisson distribution, where variance exceeded the mean of the response (White and Bennetts 1996). The negative binomial regression model took the form:

$$\ln[E(t_i)] = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} \dots + \beta_n x_{ni},$$

where $E(t_i)$ was the expected value of the number of locations within sampling unit i, β_0 represented the intercept term, $\beta_1, \beta_2, \dots, \beta_n$ represented estimated coefficients, and x_{1i}, \dots, x_{ni} were covariate values measured across respective sampling units (Nielson and Sawyer 2013a). We included multiple habitat variables likely to impact bighorn populations to assess resource selection, and quantified habitat layers (i.e., aspect, elevation, escape terrain, slope) using 10 m x 10 m resolution digital elevation data (National Elevation Dataset, USGS, Sioux Falls, SD) in a Geographic Information System (GIS) framework (ArcMap 10.1). In addition, we digitized areas impacted by fire-mediated habitat alterations using satellite imagery provided by Apollo Mapping (Boulder, CO) and with aerial photography (unpublished data WGFD 2011, 2012), both acquired shortly after each fire event (Table 4.1). Distance to burned areas were measured in meters from the center of each sampling unit to the nearest edge of burned area within the area defined as available, regardless of whether fires had yet occurred. We assessed predictor variable correlations via Pearson's correlation matrices and restricted highly correlated variables from entering model selection (|r| > 0.70) by including only the top performing variable using AIC. We further assessed multicollinearity by calculating predictor variable tolerances in top performing models (range = 0.44-0.88) and ensuring they exceeded recommended minimum tolerance thresholds (e.g., >0.10; Tabachnick and Fidell 2001). We standardized continuous predictor

variables (by *z*-score) to facilitate direct comparison of predictor variable influences in coefficient plots.

To allocate location data into the pre-fire/post-fire binary predictor used in the model, we projected pooled bighorn locations collected before the initiation of fires across the study area, quantified a response variable as a measure of intensity of use, and assigned each of the 2000 sampling unit rows the binary predictor "pre-fire" among the other calculated habitat variable values. We then repeated this procedure using pooled location data gathered after the initiation of fires labeled as "post-fire." This resulted in 4000 rows of data, with pre-fire and post-fire intensity of use equally represented in the RSF model response.

We identified seasonal timeframes representative of the Seminoe Mountain area and lifehistory adaptations similar to other low-elevation, non-migratory bighorn sheep herds in Wyoming as summer (June 1 – Oct 31) and winter (Nov 1 – April 30) seasons (Kauffman et al. 2009, Sawyer et al. 2009*b*). We used paired location data gathered from individuals that were GPS-collared both before and after fires to generate RSF models for female bighorn during summer and winter seasons. We conducted model selection using the best subset of predictor variables with competitive models Δ AIC \leq 4 (Arnold et al. 2010) as well as consideration of models with the highest Akaike's model weights (ω_i ; Burnham and Anderson 2002). We report model fit statistics for the top 3 performing models of female bighorn habitat selection for each season (Table 4.2). Due to insufficient sample sizes, male bighorn habitat selection models were not considered.

Assuming the error structure of residual values were not appropriate to generate reliable variances for model coefficients, we implemented random-*x* resampling (Fox 2002) in a bootstrapping framework to assess model coefficient variability (Efron 1979, Khurshid et al.

2005). Bootstrapping methods reflected Type 2 resource selection (Thomas and Taylor 2006), where discrete animals were the experimental units to account for individual variation in RSF models. We randomly selected the same number of animals present in the original sample (with replacement), and used locations from these animals to populate response variables within the best models and generate new variable coefficient point estimates and associated standard errors. We estimated 95% confidence intervals by encapsulating the mid-95th percentile of each coefficient under 1000 bootstrap iterations. We validated RSFs by populating top model response variables using location data from independent (unpaired) bighorn sheep that collected data either before or after habitat alterations. We then assessed whether coefficient point estimates fell within the bootstrapped confidence intervals generated from paired data. Finally, we determined significant habitat selection of fire-altered habitats if bootstrapped confidence intervals for the interaction term did not include zero, and we created coefficient plots for visual comparisons among other predictor variables.

Due to lack of location data required to conduct RSF modeling for each treatment area independently, we implemented habitat selection methods with *ad hoc* analyses that quantified the proportion of locations within fire areas. We used paired location data gathered from bighorn sheep and conducted paired *t*-tests to identify changes in the proportion of locations identified in treated areas before and after fires. We visually assessed normality of residuals and tested for equal variance among samples using Levene's test (O'Brien 1981). We implemented $\alpha = 0.05$ for statistical significance and report mean, standard error, and range for each estimate. Unlike the RSF models, we used paired data from males and females irrespective of season, and conducted tests that treated each fire independently to identify changes in proportion of locations among prescribed burns or wildfire as an indication of effectiveness of treatment type for

bighorn selection. We conducted RSF statistical analyses and data management in R 2.15.3 (R Development Core Team 2012).

Survival Analysis

To properly assess how changes within an ecosystem impact wildlife populations requires quantification of spatially-driven responses such as distribution and habitat selection, but also linking demographic responses as indicators of animal fitness. Demographic responses can be assessed in many forms as an index of animal fitness including fat reserves, pregnancy rates, recruitment, or survival, among others. We used a Kaplan–Meier product-limit estimator (K-M; Kaplan and Meier 1958) modified for staggered entry (Pollock et al. 1989) and with variances computed following Greenwood (1926) to evaluate bighorn survival throughout the study period, encompassing the 3 bighorn translocation efforts (Dec. 2009, Jan. 2010, and Dec. 2010), as well as the December 2011 capture event until all GPS units detached from animals by June 2013. We also report cause-specific mortalities documented from field observations of marked individuals throughout the study period. Finally, we conducted a series of independent t-tests to correlate bighorn survival and cause-specific mortality with a suite of variables, including variation in spatial responses of bighorn after fire (i.e., proportion of home range overlap with treated areas, selection for treated areas by a change in proportional use in treatment areas after fires, and home range expansion as the relative change in home range size after fires) as well as bighorn ages estimated during the capture event. Although we investigated incorporating survival data in more complex modeling environments (e.g., logistic regression, Cox proportional hazard models), we lacked adequate sample sizes necessary to gain population-level inference from these modeling techniques.

Though the K-M and cause-specific data showed trends through the entire study period, tests only included data recovered from bighorns that were captured within the study area in 2011 (n = 24) that were potentially influenced by fire, and for which we used the estimated age of the bighorns at capture and calculated the relative proportion of home ranges that overlapped treated areas. We further restricted samples in cases where spatial changes before and after fires were quantified at an individual level using paired data (n = 16), including the change in home range size after fires (home range expansion) and the change in the proportion of locations within treated areas after fires as an index of selection. We categorized cause-specific mortality into 2 groups that included the animals that died in connection with poor body condition (n = 4) and grouped remaining mortalities into an "other" category (n = 5). Tests with these 9 bighorn were implemented under the same assumptions and techniques as described in RSF methods.

RESULTS

Distributional Alterations in Response to Fire

Because the difference in relative home range size was quantified by dividing post-fire by prefire area, a metric equal to one indicated no relative change in home range size (Chapter 3, Fig. 3.6A). Variation was evident among individual bighorns; however, the mean change in home range size for 16 paired (i.e., pre and post-fire) bighorn showed an approximate 200% increase in home range size consistently from full home range extents to highest intensity of use (core range) areas (Chapter 3, Fig. 3.6A). When assessing the proportion of post-fire home ranges that overlapped pre-fire home range areas, home ranges quantified at the full extent averaged 50% overlap with paired home ranges before the initiation of burns. This trend decreased to ~25% overlap at extreme core range levels (Chapter 3, Fig. 3.6B). Finally, we found consistency across isopleths in the mean proportion of post-fire distributions (n = 24) that overlapped treated areas of approximately 30% (Fig. 4.2).

Habitat Selection of Treated Areas

We report paired datasets from 12 adult female bighorn to provide RSF model coefficient point estimates, standard errors, and 95% confidence intervals for summer and winter season models (Table 4.3). Location data used in the summer model included 11,573 total locations (mean per animal = 964, range = 579–1,487), while winter model data consisted of 24,620 total locations (mean per animal = 2,052, range = 1,622-2,640). Model selection procedures resulted in only slight differences in top performing model structures between summer and winter models (Table 4.2). In both cases, top models ranked well above competing model structures, outperforming competitive models by exhibiting $\omega_i \ge 0.998$, and \triangle AIC of 43.1 and 13.2 for summer and winter models, respectively (Table 4.2). Coefficient plots revealed confidence intervals encompassed point estimates from non-paired location data from n = 20 (9,605 total locations, mean per animal = 480, range = 82–741) and n = 24 (20,504 total locations, mean per animal = 854, range = 215–1480) individuals in the summer and winter seasons, respectively, indicating that models validated well when tested with supplemental bighorn location data (Fig. 4.3). Summer and winter resource selection were highly similar overall, with female bighorn selecting for lower elevation habitats, and for east, south, and west aspects in relation to the north aspect reference (Fig. 4.3). High correlation between sampling unit slope and distance to escape terrain resulted in one variable constrained from inclusion in the same models during model selection procedures. However, bighorn selected for habitat with greater slopes in the summer model, and similarly selected against increasing distances from escape terrain in winter models, supporting bighorn reliance on close proximity to steep and rugged terrain (Fig. 4.3). Female bighorn were also

similar in selecting for increased distances from roads, although only significantly in the winter season model. Differences between pre-fire and post-fire locations were identified in the winter model as well. In both models, no influence was found in the distance to burned areas, which was unsurprising because distances to treated areas were partly represented by response variables calculated before burning actually occurred. Therefore, distance to burned areas would be expected as an influential covariate only if an overall affinity or avoidance of treatment areas existed for bighorn independent of habitat alterations. Finally, the interaction term we defined as the primary indicator of selection for treated areas after habitat alterations showed no influence on bighorn resource selection, with confidence intervals overlapping zero, and validation point estimates opposite point estimates derived in model construction (Fig. 4.3).

We conducted *ad hoc* analyses in the form of paired *t*-tests as a rudimentary tool to corroborate negative binomial RSF results and to identify if different proportions of bighorn locations fell within burned areas among individual habitat treatments. An initial paired *t*-test mimicking RSF modeling compared the difference in proportion of locations within combined burned areas before and after the intiation of fires during May 2011. Similar to the results from habitat selection models, the proportion of locations before (mean = 0.23, SE = 0.06, range = 0.00–0.74) and after intiation of habitat alterations (mean = 0.30, SE = 0.05, range = 0.00–0.65) showed no difference when measured among combined fire events and before and after the initiation of fires in May 2011 ($t_{15} = 1.63$, P = 0.123). However, treating each fire independently provided some inference to specific use of treatment type by bighorn sheep. To be included in the sample, these tests required that animal locations be positively identified within independent treatment areas before, after, or before and after each fire. Results indicated that bighorn sheep significantly increased use of habitats altered with prescribed fires in 2011 and 2012 (Table 4.4).

The first prescribed burn in May 2011 resulted in an estimated increased use of 11%, with all 11 individuals increasing the proportion of locations within the burned area after the treatment. The second prescribed fire in March 2012 showed similar results, with an estimated increase of 7%, and with 9 of 10 bighorns increasing proportional use. However, we found no difference in use of burned habitat from the wildfire event in July 2012 where although 5 of 9 bighorns increased proportional use, these changes ultimately resulted in an estimated 1% decrease in area used by bighorn after the wildfire event.

Demographic Responses

We documented 14 bighorn sheep mortalities from December 2009 to June 2013. One mortality, occurring shortly after the initial translocation release in December 2009, was attributed to capture myopathy and therefore was left censored from Kaplan-Meier survival estimation conducted throughout the study period (Fig. 4.4). Predation events were primarily attributed to mountain lions (*Puma concolor*; 4 of 5 documented predations). Other causes of mortality included an apparent fall from a cliff during the winter 2010–2011, one bighorn caught in a wire fence during winter 2012–2013 (the only male mortality documented), and one unknown mortality in summer 2013. A notable portion of mortality occurred during early spring 2012, where 5 bighorn died during adverse weather events. On further examination, these animals had little to no apparent fat reserves, resulting in extreme emaciation, and examination of bone marrow content collected from femurs further indicated signs of overall poor body condition. Although survival estimates remained relatively high early in the study, the mortalities documented in 2013 resulted in a precipitous decrease in survival, and resulted in ~30% mortality from sampled bighorns during that time.

Due to the marked decrease in bighorn survival after fire-mediated habitat alterations that occurred within the study area, we conducted a series of tests to identify potential correlations between overall survival and the cause of specific mortalities and various bighorn attributes and responses to altered habitats. When comparing bighorns that died (n = 9) with those that survived (n = 15), we found bighorn mortality was correlated with older-aged animals (Table 4.5). Bighorns that died also increased their home range sizes to a higher degree than bighorns that survived after fires (Table 4.5). However, neither correlations were significant when compared with the cause of mortality from bighorns that died. In addition, test results indicated that the change in proportion of locations in treated areas after fire was not significantly different between bighorns that survived or that died, or on the cause of death from bighorn mortalities (Table 4.5). Finally, we found some evidence to suggest bighorns that died had a higher proportion of home ranges that overlapped treated areas (P = 0.146), and further, that bighorn mortality associated with poor body condition had significantly higher home range overlap with burned areas (P = 0.045; Table 4.5).

DISCUSSION

We implemented a structured approach to describe the impacts of fire-mediated habitat alterations to bighorn sheep in our study area. We analyzed changes in distribution, quantified how much treated area was used by bighorns, and investigated selection for treated habitats. We correlated these responses to bighorn survival, and through this process we found evidence that treatment type (i.e., prescribed or wild fire) likely had differing provisional impacts to overall bighorn success because prescribed fires are conducted with increased control over the timing and spatial extent of the burn. Evidence suggests that increased energy demands of animals requires larger areas for food gathering (McNab 1963), and that animals often increase home

range size when nutritional resources are scarce (Ford 1983, Tufto et al.1996). Accordingly, an inverse relationship often exists between available forage biomass or food resources and home range size (Anderson et al. 2005, Corriale et al. 2013). Thus, although our prediction that bighorns would expand distribution was supported, it may have been under negative implications on bighorn fitness. Under these assertions, if habitat quality had improved, bighorns might have restricted pre-fire distributions if they positively responded to habitat treatment conducted within current home ranges—able to access important resources while limiting energy expenditures.

Results from distributional responses indicated that bighorns within our study area uniformly expanded their post-fire home range area across isopleth levels, with increasing space use after fire at the expense of lower intensity of use within pre-fire core areas. While insightful to overall space use, changes in home range size gave little indication of changes in the spatial arrangement of distributions across the landscape. However, when examining home range overlap, bighorns also exhibited a change in the relative proportion of post-fire distribution that overlapped the corresponding pre-fire distribution in a decreasing trend from approximately 50% to 25% at increasing core range isopleths (Fig. 4.2B). This relative proportion of overlap was likely influenced by the increase in home range size, with much pre-fire distribution within the extent of post-fire areas. Notwithstanding, it rendered a relative expansion of home range that increased proportionally across increasing core area levels. These findings lend support to our prediction that habitat treatments should cause an increase in space use by bighorn sheep, and an expansion of home range areas in the study area. The identified expansion in home range sizes could be attributed to bighorns partitioning overall space use by increasing use of adjacent areas with improved habitat after treatments, while maintaining a portion of original space use due to other essential habitat requirements (e.g., proximity to escape terrain). On the contrary, bighorn

expansion may be an indication that bighorns attempted to avoid burned habitats, but were unwilling to venture far from other vital habitat components.

Although home range area increased after fires, RSF modeling showed no significant selection observed for burned areas. This may have been partly due to the inability to test selection for each fire independently during RSF modeling. Supplemental analyses testing the change in proportion of locations observed in treated areas after fires did find that bighorn use increased after both prescribed burn treatments in those areas, but not within the wildfire. While fire may have influenced habitat selection, these tests did not account for the suite of additional habitat variables that influenced habitat selection as shown in RSF models. Also, treating each fire event independently may overlook the influence one fire may have had on another. For example, bighorn may not have selected for one fire because of current affinity for a previously treated habitat, or may have avoided one area only to be confined to another. Habitat selection for fires may also have been obscured by the extensive area or spatial coverage of burns, which encompassed much bighorn distribution before and after fires within the study area. In this case, bighorn selection would not be easily identified by change in use patterns. These results left our second prediction unanswered in a sense that we were unable to positively identify habitat selection for treated areas overall, although we did find some support for bighorn selection for areas treated with prescribed burning.

A key assumption within all habitat section models is that animals will select habitat in a method to benefit overall fitness (Manly et al. 2002), and it is here we used analyses correlating demographic response of bighorn sheep to measured responses in distributional shifts and potential habitat selection. Kaplan-Meier survival estimates showed survival decreased more after the initiation of habitat alterations than before (Fig. 4.4), and identifying poor body

condition tied to mortality incidence after the wildfire event implicated habitat treatments in decreasing foraging efficiency of some bighorn sheep. After fire events, bighorn sheep that increased home ranges had a higher rate of mortality than those that expanded home ranges to a lesser degree, and the proportion of home ranges that overlapped burned areas was suspected to influence overall survival rate, and verified in animals that died from poor body condition (Table 4.5). These results seem to fall in line with the example previously described, where bighorns expanded home ranges not as an opportunity to increase use of suitable habitat, but in an attempt to gain the resources required to maintain fitness levels. Thus, our prediction of high bighorn survival rates commensurate with improved habitats was not supported, and we further discuss some associated implications below.

Some predictors shown to influence home range size include body mass (Litvaitis et al. 1986, Relyea et al. 2000) and population density or group size (Trewhella et al. 1988, Erlinge et al. 1990); however, we suggest that neither apply well to the population in our study—with bighorn densities of the recently introduced herd assumed to be below density dependence, and assumed bighorn mass unchanged and relatively homogenous, as well as the conspecific affinity and gregarious nature of bighorn sheep giving little support for territory defense influencing home range sizes (Geist 1971, Wolff 1997). However, we postulate that habitat was the driving factor explaining home range expansion in our study.

Because we found 1) limited evidence supporting habitat selection for prescribed burns, 2) no evidence that selection negatively influenced bighorn survival, and 3) that the most apparent decrease in survival was documented late in the study, we determined that prescribed burning prior to 2012 likely contributed to bighorn expansion via selection for treated habitat. Although specific habitat selection through RSF modeling revealed no selection for treated areas

as a whole, increased use of this area under optimal foraging theory likely did not hinder bighorn fitness, and we found no increase in mortality during this time. However, we postulate that fires that were conducted later in the study may have negatively impacted bighorn sheep, and we provide additional evidence to support our claim.

Climate patterns for the Seminoe Mountain area show a mean 30-yr precipitation average of 36 cm annually. However, in 2012, the study area experienced extreme drought conditions, with the lowest recorded annual precipitation recorded since 1901 (<21 cm). Therefore, vegetative response after the second prescribed burn and the wildfire event was extremely low. In particular, the wildfire that occurred in July 2012 caused extensive habitat loss, decimating shrub communities in the area, and allowing sparse vegetative recovery before winter (see Fig. 4.5). We suggest that bighorn expanded distribution at this time to gain access to remaining forage but were unwilling to vacate burned areas completely, resulting in reduced fat reserves while increasing energy expenditures. Largely dependent on the size, intensity, and completeness of burns, detrimental short-term effects of fire have been described where destruction of winter browse forage or reduced availability of forage in post-fire areas can limit wildlife populations, especially in scenarios with limited alternative wintering habitats (Klein 1982, Klebenow 1985). Under these conditions, bighorn fitness was likely suppressed, leaving them vulnerable to adverse weather conditions in early 2013, where 5 of 8 mortalities were identified within a 2 day period in mid-April. While spring weather presented sporadic snow conditions, we did not expect this to impact bighorn survival to the extent that it did, and under increased fitness levels, probably would not have resulted in high bighorn mortality. Other potential explanations for these mortalities are unlikely given that we positively identified other mortality including documentation of cliff falls, predation, and fence entanglement. While disease transmission may

cause adult mortality similar to what we observed, no indication of disease was identified in multiple diagnostics conducted during each capture event, nor during bighorn observations or during necropsy procedures.

It is important to consider that our study measured provisional responses to fire, and left little time for vegetative recovery of areas burned in 2012. Hence, while impacts of prescribed fire in May 2011 were measured through 2013, the remaining fires most certainly had little time to recover before the study period ended in June 2013, especially under drought conditions. Therefore, although initial responses to fires were correlated with increased bighorn mortality, it is likely that habitat conditions will continue to recover and support bighorn population establishment.

MANAGEMENT IMPLICATIONS

Managers implementing strategies to support bighorn sheep face many challenges in planning and conducting prescribed burning. Conducting low-intensity burns in the fall or spring may be beneficial to provide recovery of vegetative communities throughout summer seasons (Knapp et al. 2009). In addition, spring ignitions often result in mosaic burns around snow-covered and low-fuel-load habitats, which can provide bighorn sheep with alternative forage until vegetation is restored in treated areas. However, the unpredictable nature of subsequent weather patterns makes optimal timing of burns difficult, with recovery of the landscape heavily dependent on the ever-increasing stochastic tendencies in climate regimes, particularly drought conditions (Hopkins et al. 1948, Wright and Bailey 1980, Engle and Bultsma 1984, White and Currie 1983). This may be especially challenging when prescribed burning is used to prevent increasing fuel loads that increase the risk of large-scale wildfire events. Given the results of our study, we recommend conducting prescribed fires before bighorn reintroductions if applicable, or

conducting prescribed burns on a relatively small scale and on a rotational basis to avoid potentially impeding bighorn foraging ability. Furthermore, if forage conditions are ample but objectives are set to support bighorn populations by opening habitats restricted by timber encroachment, mechanical treatments such as clear-cut logging has been shown to increase habitat use by bighorns to a higher degree than burning alone (Smith et al. 1999), and should be given consideration over prescribed fire.

ACKNOWLEDGMENTS

We thank S. E. Albeke, C. B. Buchanan, M. E. Dillon, T. L. McDonald, K. T. Smith, K. L. Taylor, and L. A. Varelas of the University of Wyoming for support in data management and analysis techniques. G. S. Hiatt, D. D. Bjornlie, and B. A. Brinegar, Wyoming Game and Fish Department, provided logistical, field, and analytical support. We thank France Flying Service and Sky Aviation, as well as local landowners for study area access. The University of Wyoming, Wyoming Game and Fish Department, Wyoming Governor's Big Game License Coalition, and Wyoming Wild Sheep Foundation provided funding.

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Table 4.1. Descriptions of candidate habitat variables available to model bighorn resource selection in relation to fire in the Seminoe Mountains, Wyoming, USA, 2009–2013.

Covariates	Description
aspect	Categorical variable of dominant aspect (cardinal direction) within each sampling unit. North used as reference factor.
dist_burn	Distance from sample unit center to nearest burned habitat edge calculated after fire events (m)
dist_escp	Distance from sample unit center to nearest escape terrain (slope >27°)* (m)
dist_road	Distance from sample unit center to nearest road (m)
dist_water	Distance from sample unit center to nearest perennial water source (m)
elev	Average elevation (m) within each sampling unit
slope	Average slope within sampling unit (°)
pre.post	Binary variable ($1 = after habitat treatment; 0 = prior to habitat treatment)$
Int	Interaction term (pre.post \times dist_burn)

^{*(}DeCesare and Pletscher 2006)

Table 4.2. Model fit statistics for the top 3 seasonal models for female bighorn negative binomial RSFs in the Seminoe Mountains, Wyoming, USA, 2009–2013. Table includes season, RSF model structure, number of parameters in each model (K), Akaike's information criterion (AIC), difference in AIC from the top model (Δ AIC), and Akaike's weight (ω_i). Models were ranked based on lowest AIC values and Akaike's weight under best subset model selection procedures.

Season	Model structure	K	AIC	ΔAIC	Akaike's weight (ω_i)
Summer	aspect + dist_burn + dist_road + elev + pre.post + slope + Int	8	13429.700	0.000	1.000
	aspect + dist_burn + dist_road + elev + pre.post + slope	7	13472.800	43.100	0.000
	aspect + dist_burn + dist_road + dist_water + elev + pre.post + slope + Int	9	13489.000	59.340	0.000
Winter	aspect + dist_burn + dist_escp + dist_road + elev + pre.post + Int	8	17508.800	0.000	0.998
	aspect + dist_burn + dist_escp + dist_water + elev + pre.post + Int	8	17522.000	13.200	0.001
	aspect + dist_burn + dist_escp + dist_road + dist_water + pre.post + Int	8	17527.700	18.920	0.000

Table 4.3. Resource selection modeling results, including covariate estimates and bootstrap-derived standard errors and 95% confidence intervals, for female bighorn sheep in the Seminoe Mountains, Wyoming, USA, 2009–2013.

				95% Confid	ence interval
Season	Covariate	Estimate	SE	Lower limit	Upper limit
Summer	intercept	-0.582	NA	NA	NA
	aspect				
	east	0.743	0.127	0.537	0.979
	south	2.159	0.409	1.202	2.917
	west	1.134	0.295	0.408	1.587
	dist_burn	-0.700	1.258	-1.943	0.419
	dist_road	0.678	0.267	-0.026	1.003
	elev	-0.854	0.126	-1.059	-0.570
	pre.post	0.487	0.759	-0.056	2.115
	slope	0.704	0.176	0.396	1.054
	Int	-0.671	0.825	-2.292	0.423
Winter	intercept	0.820	NA	NA	NA
	aspect				
	east	0.651	0.313	0.177	1.126
	south	2.064	0.897	1.171	2.835
	west	0.524	0.733	0.058	1.369
	dist_burn	-0.111	0.615	-1.223	0.697
	dist_escp	-0.540	0.122	-0.784	-0.318
	dist_road	0.426	0.305	0.086	1.009
	elev	-0.453	0.718	-1.298	-0.013
	pre.post	0.311	0.285	0.043	1.060
	Int	-0.714	0.468	-1.282	0.148

Table 4.4. Results (estimates, standard errors [SE], range in estimates, df, and *P*-values) from paired *t*-tests of the proportion of bighorn locations within treated areas before and after fire events in the Seminoe Mountains, Wyoming, USA, 2009–2013.

	Pre-fire			Post	-fire				
Habitat treatment	Est.	SE	range	Est.	SE	range	df	t stat	P
Prescribed burn (May 2011)	0.03	0.01	0.00-0.10	0.14	0.02	0.01-0.28	10	-5.98	≤0.001
Prescribed burn (March 2012)	0.06	0.01	>0.01–0.11	0.14	0.02	>0.01–0.19	9	-5.37	≤0.001
Wildfire (July 2012)	0.24	0.08	0.00-0.69	0.23	0.09	0.00-0.54	8	0.30	0.771

Table 4.5. Results of independent 2-sample *t*-tests for survival and cause-specific mortality of bighorn sheep after the initiation of fire-mediated habitat alterations in the Seminoe Mountains, Wyoming, USA, from May 2011–June 2013.

		Survi	ved		Di	ied			
Variable	Est.	SE	range	Est.	SE range		df	t stat	P
Relative home range (95% contour) increase after fires	1.48	0.36	0.24–3.40	5.48	1.64	2.60-12.80	14	2.69	0.018
Estimated capture age	4.13	0.70	1–10	7.44	0.88	2–11	22	2.93	0.008
Relative home range (95% contour) overlap with treated area	0.25	0.04	0.00-0.48	0.36	0.06	0.00-0.51	22	1.51	0.146
Selection for treated habitat (change in proportion of locations within treated areas after fires)	0.06	0.07	-0.41-0.38	0.08	0.05	-0.09-0.28	14	0.26	0.801
			Cause-specifi	c mortali	ity				
	Po	or body o	condition		Ot	her			
Variable	Est.	SE	range	Est.	SE	range	df	t stat	P
Relative home range (95% contour) increase after fires	5.08	2.63	1.34-10.15	5.79	2.42	2.54-12.80	5	0.19	0.854
Estimated capture age	7.25	0.48	7–8	7.60	1.63	2–11	7	0.18	0.859
Relative home range (95% contour) overlap with treated area	0.48	0.03	0.39-0.53	0.26	0.07	0.00-0.39	7	-2.44	0.045

Table 4.5 (continued).

	Po	or body o	condition	Other			_		
Variable	Est.	SE	range	Est.	SE	range	df	t stat	\boldsymbol{P}
Selection for treated habitat (change in proportion of locations within treated areas after fires)	0.00	0.04	-0.09-0.05	0.15	0.06	0.00-0.29	5	1.81	0.130

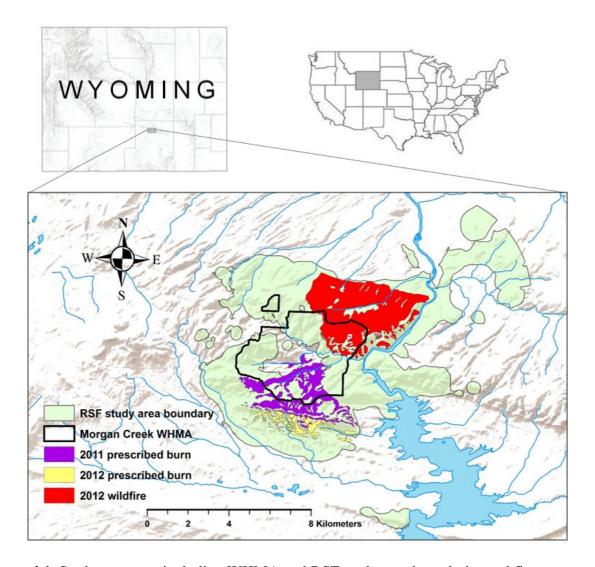


Figure 4.1. Study area map including WHMA and RSF study area boundaries and fire events from 2011–2012 in the Seminoe Mountains, south-central Wyoming, USA.

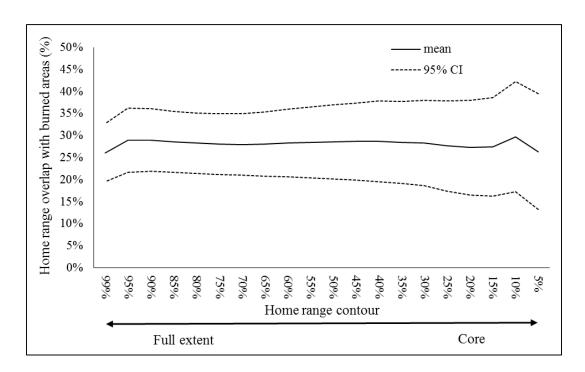


Figure 4.2. Proportion of 24 bighorn home range distributions that overlapped fire-treated areas after the initiation of burns in the Seminoe Mountains, WY, USA, May 2011–June 2013.

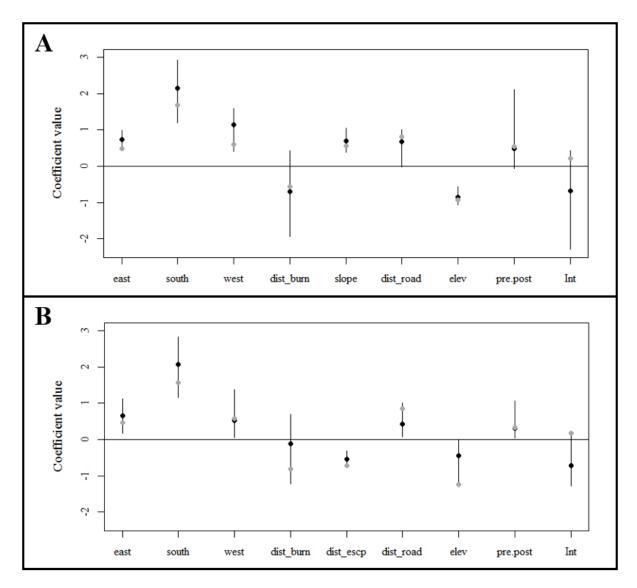


Figure 4.3. RSF model coefficient plots for female bighorn resource selection in the Seminoe Mountains, Wyoming, USA, 2009–2013. (A) Summer habitat selection. Point estimates and bootstrap-derived 95% confidence intervals were based on n = 12 individuals (black), and validation estimates from n = 20 individuals (grey points). (B) Winter habitat selection. Point estimates and bootstrap-derived 95% confidence intervals were based on n = 12 individuals (black), and validation estimates from n = 24 individuals (grey points). Note the confidence intervals for interaction terms (far right) overlap zero, indicating bighorn sheep did not select fire-treated habitats after burns during summer or winter seasons.

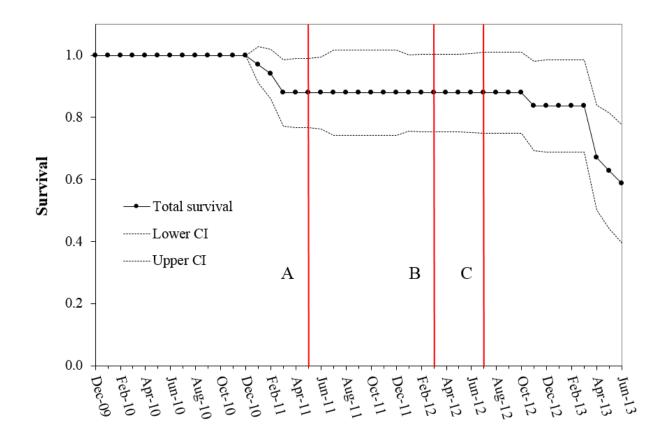


Figure 4.4. Staggered-entry Kaplan–Meier survival estimates of radio-collared bighorn sheep in the Seminoe Mountains, Wyoming, USA, 2009–2013. Vertical lines represent fire events including (A) May 2011 prescribed fire, (B) March 2012 prescribed fire, and (C) July 2012 wildfire.

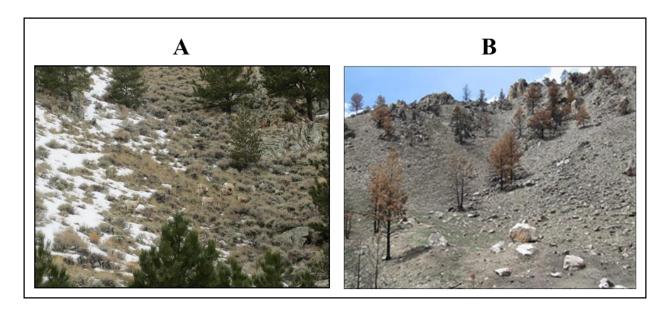


Figure 4.5. Photos of a northeast-facing slope in Hamilton Creek taken before and after a wildfire event in the Seminoe Mountains, Wyoming, USA in July 2012. A) Photo taken Nov 2011 before wildfire event. Note bighorn sheep in mixed sagebrush habitat. B) Photo taken Nov 2012 after wildfire event. Note complete removal of shrub component with little available forage proceeding winter season.

APPENDIX A. Table of information collected from 3 bighorn sheep translocations to the study area during 2009 and 2010, as well as study area captures that occurred in 2011 where bighorn were captured and released on-site in the Seminoe Mountains, Wyoming, USA. Shaded area indicates captures that occurred in the Seminoe Mountains study area.

ID	Source/origin	Release date	Sex	Capture age	Fix-rate/duration	GPS success	# locations
1	Diablo	12/2/2009	M	3.5	1hr/6 months	94%	3500
2	Diablo	12/2/2009	M	2.5	1hr/6 months	95%	3929
3	Diablo	12/2/2009	F	8	1hr/6 months	97%	4027
4	Diablo	12/2/2009	F	8	1hr/6 months	98%	4086
5	Diablo	12/2/2009	F	6	1hr/6 months	98%	4073
6	Diablo	12/2/2009	M	3.5	1hr/6 months	96%	3982
7	Diablo	12/2/2009	F	6	1hr/6 months	96%	3994
8	Diablo	12/2/2009	F	7	1hr/6 months	96%	3983
9	Diablo	12/2/2009	F	4	1hr/6 months	94%	3907
10	Diablo	12/2/2009	F	6	5hr/18 months	84%	2166
11	Diablo	12/2/2009	F	5	5hr/18 months	100%	26
12	Diablo	12/2/2009	F	3	5hr/18 months	93%	2407
13	Diablo	12/2/2009	F	3	5hr/18 months	94%	2414
14	Devil's Canyon	1/30/2010	M	2	5hr/18 months	96%	2190
15	Devil's Canyon	1/30/2010	F	6	5hr/18 months	90%	2061
16	Devil's Canyon	1/30/2010	F	3	5hr/18 months	99%	1589
17	John Day River	12/2/2010	M	2	5hr/18 months	94%	2423
18	Devil's Canyon	1/30/2010	F	1	5hr/18 months	93%	2247
19	Devil's Canyon	1/30/2010	F	4	5hr/18 months	94%	2264
20	Devil's Canyon	1/30/2010	F	5	5hr/18 months	96%	1168
21	Devil's Canyon	1/30/2010	F	5	5hr/18 months	96%	2336
22	Devil's Canyon	1/30/2010	F	3	5hr/18 months	96%	753
23	John Day River	12/2/2010	F	6	5hr/18 months	83%	367
24	John Day River	12/2/2010	F	7	5hr/18 months	93%	320
25	Devil's Canyon	1/30/2010	F	1	1hr/6 months	97%	3243
26	Devil's Canyon	1/30/2010	M	3	1hr/6 months	96%	3224

Appendix A (continued).

ID	Source/origin	Release date	Sex	Capture age	Fix-rate/duration	GPS success	# locations
28	Devil's Canyon	1/30/2010	F	2	1hr/6 months	99%	3310
29	John Day River	12/2/2010	F	1	1hr/6 months	95%	4531
30	John Day River	12/2/2010	F	6	1hr/6 months	98%	4663
31	John Day River	12/2/2010	F	6	1hr/6 months	95%	4549
32	John Day River	12/2/2010	F	5	1hr/6 months	96%	4567
33	John Day River	12/2/2010	M	1	1hr/6 months	83%	3995
34	John Day River	12/2/2010	F	5	1hr/6 months	96%	4564
35	John Day River	12/2/2010	F	7	1hr/6 months	94%	4462
36	John Day River	12/2/2010	M	1	1hr/6 months	97%	4654
37	John Day River	12/2/2010	F	1	1hr/6 months	96%	4601
38	John Day River	12/2/2010	F	8	5hr/18 months	90%	416
39	John Day River	12/2/2010	F	5	5hr/18 months	NA	NA
40	John Day River	12/2/2010	F	7	5hr/18 months	91%	2453
3	Diablo	12/2/2011	F	10	5hr/18 months	93%	2013
4	Diablo	12/2/2011	F	10	5hr/18 months	96%	2567
7	Diablo	12/3/2011	F	8	5hr/18 months	87%	2095
8	Diablo	12/2/2011	F	9	5hr/18 months	94%	2391
9	Diablo	12/2/2011	F	6	5hr/18 months	85%	2348
10	Diablo	12/3/2011	F	8	5hr/18 months	89%	2131
12	Diablo	12/2/2011	F	5	5hr/18 months	93%	2528
14	Devil's Canyon	12/3/2011	M	4	5hr/18 months	83%	2365
18	Devil's Canyon	12/2/2011	F	3	5hr/18 months	83%	2286
19	Devil's Canyon	12/3/2011	F	6	5hr/18 months	96%	2535
22	Devil's Canyon	12/3/2011	F	5	5hr/18 months	93%	2520
25	Devil's Canyon	12/3/2011	F	3	5hr/18 months	85%	2329
26	Devil's Canyon	12/2/2011	M	5	5hr/18 months	71%	2036
27	Devil's Canyon	12/3/2011	M	3	5hr/18 months	45%	1707
33	John Day River	12/2/2011	M	2	5hr/18 months	88%	1429
34	John Day River	12/2/2011	F	6	5hr/18 months	85%	2040

Appendix A (continued).

ID	Source/origin	Release date	Sex	Capture age	Fix-rate/duration	GPS success	# locations
91*	Diablo	12/2/2011	F	6	5hr/18 months	77%	2194
92*	Diablo	12/3/2011	F	7	5hr/18 months	86%	2010
93**	Seminoe Mtns	12/2/2011	F	1	5hr/18 months	90%	2458
94**	Seminoe Mtns	12/2/2011	F	1	5hr/18 months	NA	NA
95**	Seminoe Mtns	12/2/2011	F	1	5hr/18 months	81%	2265
96*	Diablo	12/2/2011	F	11	5hr/18 months	94%	2231
97*	John Day River	12/3/2011	F	AD	5hr/18 months	90%	2432
98**	Seminoe Mtns	12/3/2011	F	1	5hr/18 months	93%	2516
99**	Seminoe Mtns	12/2/2011	M	1	5hr/18 months	90%	2399

^{*} Indicates bighorn was not collared during translocation.
** Indicates bighorn born in study area.

APPENDIX B. Supplemental discussion and validation procedures for bighorn acclimation analyses conducted in Chapter 2.

Another statistical methods for documenting the acclimation period of ungulates include comparing the deviation between annual average daily movement rates and post-release movements (see Dechen Quinn et al. 2012). When conducting this method to identify postrelease acclimation periods of translocated bighorn sheep, we found post-release movements consistently merged with average bighorn movements approximately 29 days after release (Fig. B.1), which is directly comparable to our finding of 29.3 days (SE = 2.5 days) using functional data analysis. Although the Dechen Quinn et al. (2012) method yielded similar results for average acclimation period, when censoring location data, using a functional data analysis was advantageous because of its ability to estimate acclimation periods from GPS data with differing fix rates, without the need to standardize individual movement rates to create a population average. This technique also allowed acclimation periods to be estimated without the need to collect location data across multiple years to establish average movement rates for each calendar day. Finally, Dechen Quinn et al. (2012) report that improper data censoring caused significant differences in movement estimate analyses when using datasets of <90 days. Because our functional data analysis created a summary measurement for each experimental unit, acclimation time was identified for each animal, providing the ability to incorporate individual variation during data-censoring. This method allows researchers the opportunity to censor biased data individually, which is especially beneficial when analyzing short (<90 days) data sets.

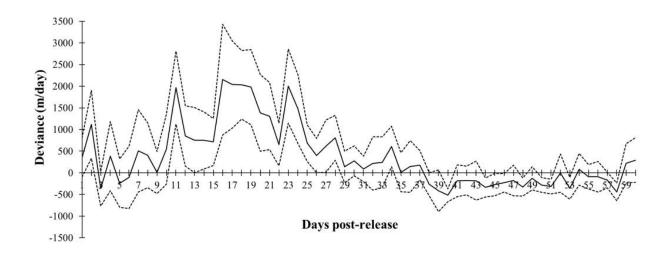


Figure B.1. Population-based estimate of acclimation period for bighorn sheep translocated to the Seminoe Mountains, Wyoming, USA. Mean deviance with 95% confidence intervals of post-release movements are compared to annual average movement rates of bighorn sheep on corresponding days from 2010–2013.

APPENDIX C. Supplemental material from chapter 4 regarding RSF analyses conducted for bighorn sheep in the Seminoe Mountains, Wyoming, USA, 2009–2013.

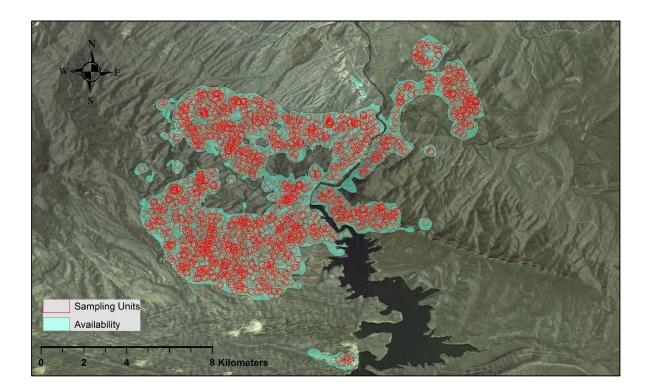


Figure C.1. RSF bighorn availability and sampling units.

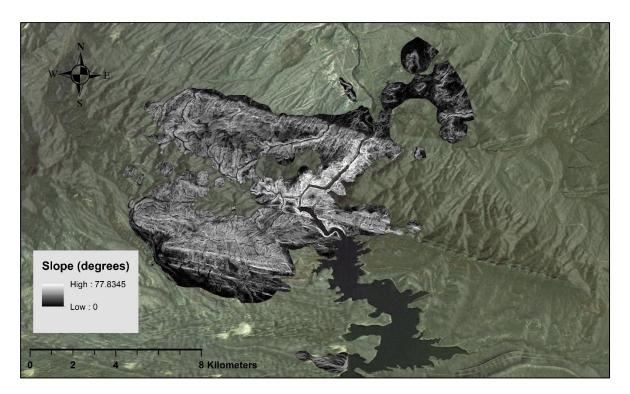


Figure C.2. RSF slope map.

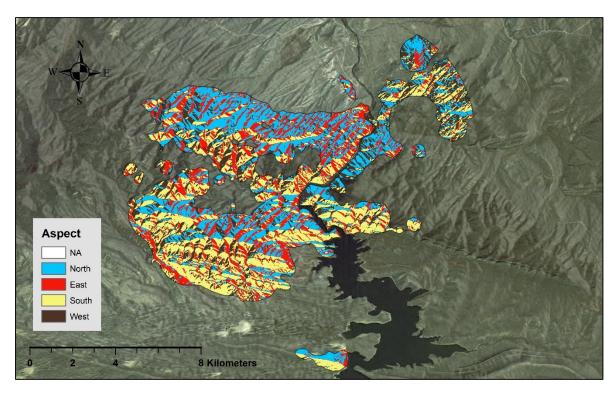


Figure C.3. RSF aspect map.

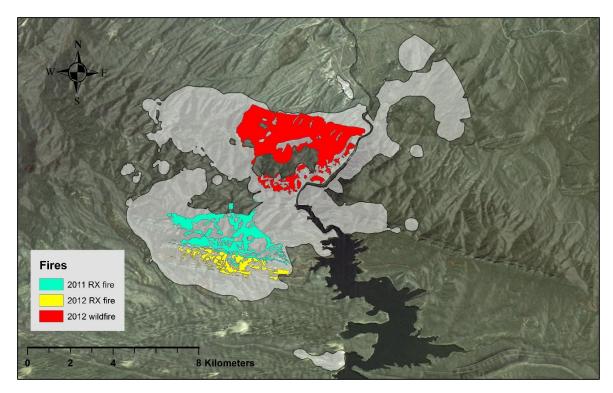


Figure C.4. RSF fire map.

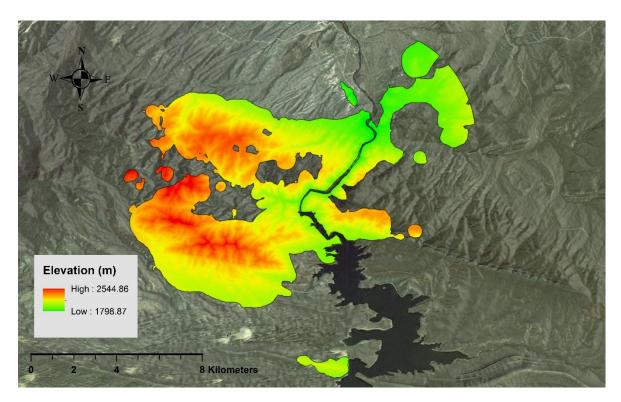


Figure C.5. RSF elevation map.

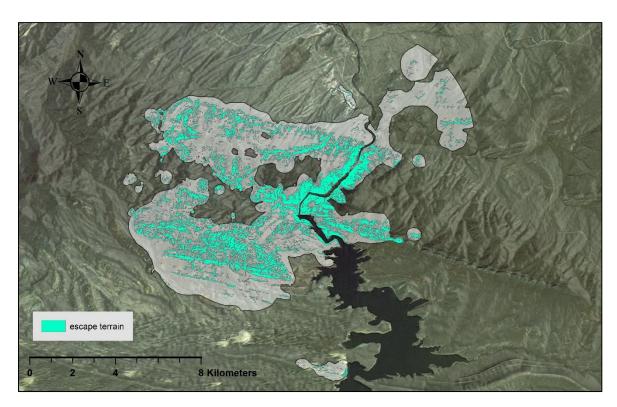


Figure C.6. RSF escape terrain map.