2008

Evaluation of an Augmentation of Rocky Mountain Bighorn Sheep at Badlands National Park, South Dakota

Teresa J. Zimmerman

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EVALUATION OF AN AUGMENTATION OF ROCKY MOUNTAIN BIGHORN SHEEP AT BADLANDS NATIONAL PARK, SOUTH DAKOTA

BY

TERESA J. ZIMMERMAN

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Major in Wildlife and Fisheries Sciences

South Dakota State University

2008
Evaluation of an augmentation of Rocky Mountain bighorn sheep at Badlands National Park, South Dakota

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Jonathan A. Jenks
Dissertation Advisor

Dr. David W. Willis
Date
Head, Department of Wildlife and Fisheries Sciences
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ABSTRACT

Evaluation of an augmentation of Rocky Mountain bighorn sheep at Badlands National Park, South Dakota

Teresa J. Zimmerman

August 2008

Audubon’s (a.k.a. Badlands) bighorn (Ovis canadensis auduboni [Merriam 1901] now O. c. Canadensis [Shaw 1804]), described as a subspecies of bighorn sheep, was extirpated from its range by 1924. In 1964, 22 Rocky Mountain bighorn sheep were translocated from Pikes Peak, Colorado, to Badlands National Park (BNP) in southwestern South Dakota. Based on the estimated effective population size and analysis of molecular data, the bighorn sheep population at BNP underwent a population bottleneck at founding. Recommendations to restore genetic diversity in the BNP population included a mixed-sex augmentation (n > 30) from an outbred, native population of Rocky Mountain bighorn sheep. Shackleton and the International Union for Conservation of Nature and Natural Resources (IUCN)/Species Survival Commission (SCC) Caprinae Specialist Group also had identified the population at BNP as a population of conservation concern and recommended expanding population size and distribution of bighorn sheep throughout their range in the eastern mixed-grass prairie. In September 2004, BNP in conjunction with the South Dakota Department of Game, Fish and Parks and the New Mexico Department of Game and Fish, captured, radio-collared
or ear-tagged, and relocated to BNP 23 (10 adult ewes, 2 yearling ewes, 5 ewe lambs, and 6 ram lambs) Rocky Mountain bighorn sheep from Wheeler Peak, New Mexico.

Because of the poor colonizing ability of bighorn sheep, previous transplant programs have attempted to reestablish populations in localized areas where they have been extirpated or to expand populations where they have been reduced. All western states in North America have reintroduced populations of bighorn sheep, yet the rate of successful establishment of self-sustaining reintroduced populations has been < 50%. If introduced bighorn sheep were monitored regularly and if each introduction was viewed as an experiment and rigorously evaluated, the rate of successful translocations may increase. The overall objective of this study was to evaluate the success of the augmentation by examining 1) survivorship, 2) lamb production, 3) dispersal, 4) 95% and 50% adaptive kernel, fixed kernel, and minimum convex polygon home-range size, 5) 95% and 50% adaptive kernel planimetric and surface area estimates, 6) interannual variation in home-range size, 7) habitat use, 8) escape terrain and buffer terrain, 9) an animal location based model (ALBM), 10) an escape terrain and buffer model (ETBM), 11) the habitat evaluation procedure (HEP) of Sweanor et al. (1995) and Zimmerman et al. (2006), 12) degree of population subdivision ($F_{st}$) between the North and South Units in BNP, 13) observed heterozygosity ($H_o$), expected heterozygosity ($H_e$), number of alleles per locus, average number of alleles per locus ($N_c$), and the number of effective alleles ($N_{ea}$) of bighorn sheep at BNP pre- and post-augmentation.

Radio-collared individuals were relocated ≥ 3 times weekly from September 2004–2007. Visual daytime locations were recorded and added to a Geographic
Information System. Genomic DNA from blood and tissue samples from resident and translocated bighorn sheep and their offspring was extracted, amplified, and typed for 15 microsatellite loci.

Eighteen of 23 translocated bighorn sheep survived and remained with the sub-population. In 2005, 10 lambs were born and 9 (5 females, 4 males) survived to 1 year of age. In 2006, 9 lambs were born and 8 (4 females, 4 males) survived to 1 year of age. In 2007, 8 lambs were born and 7 (5 females, 2 males) survived to 1 year of age. In 2006, 9 yearling first-generation offspring (F1) dispersed from BNP with straight-line dispersal distances ranging from 43 to 524 km. In 2007, 3 yearling male F1 dispersed 25 km from BNP.

The 95% adaptive and fixed kernel home-range estimates did not differ \((P = 0.096)\) and the 95% adaptive kernel home-range estimate and the minimum convex polygon estimate did not differ \((P = 0.211)\). The 50% fixed kernel home-range estimate was greater \((P = 0.001)\) than the 50% adaptive kernel home-range estimate. The 95% home-range size increased \((P = 0.007)\) between year 1 of the study and year 2 of the study, but the core estimates did not differ \((P = 0.450)\) between years. The 95% and 50% 3D surface areas of translocated sheep were greater \((P = 0.001; P = 0.001, \text{ respectively})\) than the 2D planimetric areas; the 95% and 50% surface area estimates of the resident bighorns were greater \((P = 0.027; P = 0.027, \text{ respectively})\) than planimetric areas. The 95% and 50% planimetric adaptive kernel estimates were greater \((P = 0.002; P = 0.002, \text{ respectively})\) in resident than translocated sheep.
Translocated and resident bighorn sheep were located on more vertical slopes ($P < 0.001$), closer to wet areas ($P < 0.001$), closer to roads ($P < 0.001$), and closer to escape terrain ($P < 0.001$) compared with respective random locations. Translocated bighorn sheep were located on more ($P < 0.001$) horizontal slopes, closer to wet areas ($P < 0.001$), and closer to roads ($P < 0.001$) compared with resident bighorn sheep. Translocated and resident bighorn sheep locations did not differ ($P = 0.800$) in their proximity to escape terrain. The best model to differentiate habitat use of translocated compared with resident bighorn sheep included distances to escape terrain and roads, slope, and vegetation variables.

Compared with random locations, bighorn sheep locations were in closer proximity to slopes $\geq 40^\circ$ that all other slopes evaluated and were on average within 285 m of slopes $\geq 40^\circ$. The ALBM included variables such as distances to escape terrain, roads, and water, and vegetation. Based on the odd’s ratios of the final model, bighorn sheep were located closer to $40^\circ$ slopes, roads, and wet areas compared with random locations. Bighorn sheep selected human-use areas and woodlands compared with the categorical reference (i.e., unvegetated badlands), whereas there was no selection for grasslands, shrublands, and water sources.

Within the 981 km$^2$ study area evaluated in BNP, approximately 464 km$^2$ and 367 km$^2$ of suitable bighorn sheep habitat was identified by the ALBM and ETBM, respectively. The Sweanor et al. (1995) and Zimmerman et al. (2006) models identified approximately 377 km$^2$ and 599 km$^2$, respectively, of suitable bighorn sheep habitat in
BNP. Based on the ETBM, 4,007.2 km\(^2\) of 108,362 km\(^2\) of potential bighorn sheep habitat was identified as suitable for bighorn sheep in western South Dakota.

DNA was extracted and successfully genotyped from 95 individuals from 7 time periods (e.g., bighorn sheep that occurred prior to 1925 [Historic], 1992, 1996, 1998, adult males captured prior to the augmentation [Adult04], augmented bighorn sheep [NMIntro], offspring of the augmentation [Off0506]). Seven loci from 4 populations (e.g., 1992, 1996, 1998, NMIntro) deviated from Hardy-Weinberg equilibria. The greatest substructure (i.e., \(F_{st}\)) occurred between historic samples and Adult04. Historic bighorn sheep had the lowest \(N_a\) and \(N_ea\) whereas NMIntro had the highest \(N_a\) and \(N_ea\). Polymorphic loci were lowest in Historic samples followed by Adult04. Observed and expected heterozygosity was lowest in historic bighorn and greatest in Off0506. A significant \((P < 0.001)\) excess of heterozygotes was observed in the Off0506 indicating potential outbreeding. Based on all loci of resident bighorn sheep, rate of expected heterozygosity loss was 9.8% in 1992–1998 and 5.05% in 1998–2004, with a total decrease of 1.1% per year in 1992–2004.

Although lamb:ewe ratios of bighorn sheep declined following translocation, the number of lambs produced in 2005–2007 was sufficient (>25:100 lambs:ewes) for population growth to occur. The primary factor influencing population growth during this study was poor yearling recruitment due to long-distance movements. Long-term objectives of bighorn sheep research and management at BNP should include continual visual relocations of translocated bighorn sheep and their offspring to examine survivorship, annual variability in home-range size, shifts in habitat selection, interherd
movements, and factors contributing to changes in habitat use. The augmentation was effective at increasing the genetic diversity and short-term viability of the bighorn sheep population at BNP. Concern is warranted that outbreeding depression may occur in the second generation offspring (F2) and subsequent generations. Long-term viability of bighorn sheep at BNP does not appear to be limited by genetic diversity but rather by population size. Management objectives should focus on increasing the total BNP population size to $\geq 150$ individuals.
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CHAPTER 1

SURVIVAL, LAMB PRODUCTION, AND DISPERSAL OF TRANSLOCATED
BIGHORN SHEEP AND THEIR OFFSPRING AT BADLANDS NATIONAL
PARK, SOUTH DAKOTA
INTRODUCTION

Bighorn sheep (*Ovis canadensis*) are an ecologically fragile species, which was once relatively abundant but now are one of the rarest ungulates in North American (Buechner 1960). Although mountain sheep and humans have coexisted in North America for thousands of years (Hopkins 1967, Hopkins et al. 1982), impacts of humans in ≤ 150 years have lead to major declines in bighorn sheep populations (Valdez and Krausman 1999). Bighorn sheep suffer from the same factors that face many threatened and endangered species: reduced and fragmented habitat, loss of movement corridors, loss of genetic fitness, diseases, competition, predation, and human impacts (Douglas and Leslie 1999).

The Audubon’s bighorn ecotype (*Ovis canadensis auduboni* [Merriam 1901] now *O. c. canadensis* [Shaw 1804]), described by Cowan (1940) as a subspecies of bighorn sheep inhabited the badlands of the Yellowstone and Missouri rivers in eastern Montana, eastern Wyoming, western North Dakota and South Dakota, and northwestern Nebraska (Valdez and Krausman 1999). The eastern extent of their range occurring in the South Dakota badlands (Buechener 1960). The last known Audubon’s bighorn in South Dakota, was harvested in 1924 or 1925 in Washabaugh (a.k.a. south Jackson) County, near the present day location of Badlands National Park (BNP) (Badlands National Park, National Park Service, historical record).

To restore this native ungulate to its former range, a management policy of the National Park Service (National Park Service Management Policy 2006), 22 Rocky Mountain bighorn sheep from Pikes Peak, Colorado were released into a 150-ha
enclosure in BNP in 1964 (Ramey et al. 2000). Based on the estimated effective population size and analysis of molecular data, the bighorn sheep population at BNP underwent a population bottleneck at founding, yet the population increased over the following 3 decades reaching a high of \( \approx 120 \) individuals in 1991 (Ramey et al. 2000). Recommendations to restore genetic diversity in the BNP population included a mixed-sex augmentation \((n > 30)\) from an outbred, native population of Rocky Mountain bighorn sheep (Ramey et al. 2000). Shackleton and the International Union for Conservation of Nature and Natural Resources (IUCN)/Species Survival Commission (SCC) Caprinae Specialist Group (1997) identified the population at BNP as a population of conservation concern; ecotypes of bighorn sheep in this region were not secure because of the paucity of reserves and protected areas that contained the species. Thus, conservation measures proposed by the IUCN/SCC also were to expand population size and distribution of bighorn sheep throughout their range in the eastern mixed-grass prairie (Shackleton and the IUCN/SCC Caprinae specialist group 1997).

Because of the poor colonizing ability of bighorn sheep (Douglas and Leslie 1999), transplant programs have attempted to reestablish populations in localized areas where they have been extirpated (Buechner 1960) or to expand populations where they have been reduced. All western states in North American have reintroduced populations of bighorn sheep (Shackleton et al. 1999). Yet, the rate of successful establishment of self-sustaining reintroduced populations has been \(< 50\%\) (Ramey et al. 2000). If introduced sheep were regularly monitored and if each introduction was viewed as an experiment and rigorously evaluated, the rate of successful translocations could increase
(Roy and Irby 1994, Douglas and Leslie 1999). According to Douglas and Leslie (1999) regular monitoring of population demographics (e.g., lamb:ewe ratios) is necessary to determine the success of a reintroduction. Furthermore, because population growth is influenced by emigration and mortality, information on dispersal and cause-specific mortality may aid in the understanding of population dynamics of bighorn sheep. Therefore, the objectives of this study were to document 1) survivorship, 2) lamb production, and 3) dispersal of translocated bighorn sheep and their offspring. I hypothesized that: 1) survivorship would be high due to lack of large predators and relative isolation from domestic sheep herds, 2) lamb production would initially be high then decrease in subsequent years (Lewis 1998), and 3) dispersal would be limited and male biased (Geist 1971).

**STUDY AREA**

Badlands National Park (Latitude: 43.710880, Longitude: -102.477030) encompasses 98,400 ha and is located in Pennington, Shannon, and Jackson counties within the White River badlands of southwestern South Dakota (Weedon 1999). The badland formations, which comprised 45% of BNP (Von Loh et al. 1999), consist of very fine, unconsolidated clay with thin beds of sandstone or isolated concretions (Weedon 1999). Sharp gradients in elevation (700–1,000 m) and slopes (0–71°) occur throughout the region (Sweanor et al. 1995). Topography of the badlands was formed because of the coincidence of elevation, rainfall, carving action of streams, and the substrate, resulting in slumps, natural bridges, arches, sod tables, toadstools, and isolated flat remnants of the higher plains (Weedon 1999). These vegetated slumps along with mixed-grass prairie
sod tables occur in close proximity to the steep badland terrain and are important feeding areas for bighorn sheep (Gamo et al. 1999). Temperature in the BNP ecosystem ranges from -41 to 47 C, and annual precipitation averages 41 cm (Weedon 1999).

The badlands encompass true short-grass prairie, midgrass prairie, and bunch grass types (Weedon 1999). The Western Wheatgrass Alliance was the most common vegetation association encompassing 37% of BNP (Von Loh 1999). Common species associated with this alliance included western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), blue grama (*Bouteloua gracilis*), and buffalo grass (*Buchloe dactyloides*) (Weedon 1999). Other common species included needle and thread grass (*Hesperostipa comata*), fringed sage (*Artemisia frigida*), prairie junegrass (*Koeleria macrantha*), little bluestem (*Schizachyrium scoparium*), green sedge (*A. ludoviciana*), and purple coneflower (*Echinacea angustifolia*) (Weedon 1999). Patches of Rocky Mountain juniper (*Juniperus scopulorum*) and eastern red cedar (*J. virginiana*) occur in upper protected draws and slopes (Weedon 1999). Other species such as plains cottonwood (*Populus deltoides*), peach-leaved willow (*Salix amygdaloides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and American elm (*Ulmus americana*) occur in the deciduous complex along the White River (Weedon 1999).

Although 42% of BNP is covered by prairie grasslands, > 46% is clay formations on which vegetation is sparse or absent (Von Loh et al. 1999). Yellow-sweet clover (*Melilotus officinalis*), a biennial, is the dominant legume with cover of 1.7–3.3% in sparse vegetation and 2.4–8.3% in wheatgrass prairie (Van Riper 2005).
Primary roads in BNP are narrow, asphalt based, and 2-lane. Secondary roads are gravel or unimproved dirt that are maintained by BNP. Roadside shoulders along primary and secondary roads are mowed in summer. Potential predators of bighorn sheep in BNP include coyotes (*Canis latrans*), bobcats (*Felis rufus*), and golden eagles (*Aquila chrysaetus*). Occasional sign or observations of mountain lions (*Puma concolor*) within the area have been reported (E. Childers, National Park Service, personal communication). Presence and potential impacts of mountain lions on bighorn sheep in this region are probably limited but are currently unknown. Potential herbivore competitors include bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn antelope (*Antilocapra americana*), and black-tailed prairie dogs (*Cynomys ludovicianus*).

**METHODS**

In September 2004, BNP in conjunction with the South Dakota Department of Game, Fish and Parks and the New Mexico Department of Game and Fish, captured 23 (10 adult ewes, 2 yearling ewes, 5 ewe lambs, and 6 ram lambs) Rocky Mountain bighorn sheep from Wheeler Peak, New Mexico. Bighorn sheep were captured via baited dropnets and darting (Jessup et. al 1984, Kock et al. 1987). Ewes were aged based on tooth eruption (Taylor 1962) and wear. Adult and yearling ewes were fitted with colored very high frequency (VHF150–151 MHz) radio transmitters (250 grams and 1.5 lbs—Advanced Telemetry Systems, Isanti, Minnesota). Lambs were marked with numbered red, yellow, or orange ear tags and were later fitted with VHF radiocollars. Captured bighorn sheep were released at Conata Basin Picnic Area near Pinnacles in BNP between
24–27 September 2004. Pinnalces was selected as the release site because it had been identified as a site with suitable habitat (Sweanor et al. 1995) and contained a subpopulation comprised of 15 individuals (9 rams, 3 ewes, 1 yearling, and 2 lambs) based on a 2003 ground survey (E. Childers, National Park Service, personal communication). From November 2005–2006, 5 (2 male, 3 females) first generation offspring (F1) were captured using a net-gun and eartagged. Three female F1 bighorn sheep were captured and radiocollared from November 2006 to May 2007. Capture and handling methods followed recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (1998) and were approved by the South Dakota State University Institutional Animal Care and Use Committee.

Translocated bighorn sheep had been habituated to humans in their former range and therefore, could be observed from close range (5–25 m) allowing for recording of visual relocations at BNP. Radiocollared individuals were relocated ≥ 3 times weekly from September 2004 to 2007 using handheld and omni directional antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA). Visual daytime locations (Fairaizl 1980), group composition, and behavior (e.g., feeding, bedded, walking) were recorded. All individuals within the group were identified by radiocollar color, ear tag, or distinguishable markings. Universal transverse mercator (UTM-Zone 13) position of the individual or group was calculated based on the UTM of the observer collected using a handheld GPS, distance to the animal using a Leica© 1200 rangefinder (Leica Camera AG, Solms, Germany) accurate to ± 1 m, azimuth using a compass, and the vertical angle of the line of sight using a clinometer.
Locations of dispersing yearlings were entered into a Geographic Information System, and HOME-RANGE TOOLS ANALYSIS EXTENSION (Rodgers et al. 2005) in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) was used to create paths of straight-line movements between locations. Distances between locations were calculated using HAWTHS TOOLS (Beyer 2004).

I followed the management recommendations of Gross et al. (2000) to reduce the potential for disease transmission between domestic sheep and bighorn sheep. Management guidelines, recommended that a buffer of 13.5–16 km occur between domestic sheep and bighorn sheep to prevent disease transmission through direct or aerial contact (Desert Bighorn Council 1990; United States Department of the Interior, Bureau of Land Management 1998). Bighorn sheep located within the recommended buffer were euthanized to circumvent disease. Euthanized animals were sent to the South Dakota Animal Disease Research and Diagnostics Laboratory or the Wyoming State Veterinary Laboratory for disease testing. Riney (1955), and total kidney fat indices were used to assess body condition of dispersing bighorn sheep.

RESULTS

Survival

Eighteen of 23 translocated bighorn sheep survived and remained with the sub-population (Table 1). On 5 May 2005, 2 of 5 female lambs and 1 of 6 male lambs were not observed with the translocated population. I had assumed these individuals were dead until 17 November 2005 when the male returned and was observed with the translocated population. The 2 females were not observed after May 2005, and were
assumed dead. During summer 2005, 1 adult female (43D) died due to a vehicle collision and 1 adult female (36D) died of unknown causes. During October 2007, a 3.5-year-old female, translocated as a lamb, died of unknown causes. Remaining individuals survived through the extent of the study period.

Table 1. Survivorship of bighorn sheep translocated to Badlands National Park, South Dakota, USA, in 2004–2008.

<table>
<thead>
<tr>
<th>Age (2004)</th>
<th>No.</th>
<th>Sex</th>
<th>Mortality # (Year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>≥ 1.5 years</td>
<td>12</td>
<td>Female</td>
<td>2 (2005)</td>
</tr>
<tr>
<td>≤ 6 months</td>
<td>6</td>
<td>Male</td>
<td>0</td>
</tr>
<tr>
<td>≤ 6 months</td>
<td>5</td>
<td>Female</td>
<td>2 (2005)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 (2007)</td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>--</td>
<td>5</td>
</tr>
</tbody>
</table>

Lambing

In summer 2005, 10 females (8 of 10 adults; 2 of 2 two-year-olds) lambed 11 May to 26 June. One lamb died of unknown causes 16–25 July 2005 resulting in a 3-month-old lamb:adult ewe ratio of 75:100, (Table 2). All nine lambs that survived to 3 months of age (5 females, 4 males) also survived to age 1 year.

In summer 2006, 9 females (7 of 10 adult females; 2 of 3 two-year-old females) lambed from 23 May to 19 June. The 2 ewes (#34 and #41) that were not observed with lambs in 2005, also were not observed with lambs in 2006 (Appendix 1). Ewe #7 was observed with a lamb on 25 May 2006, but the lamb was not seen again, resulting in a 3-month-old lamb:adult ewe ratio of 62:100,. All 8 lambs (4 females, 4 males) that survived to 3 months of age also survived to age 1 year.
In summer 2007, 8 females (7 of 13 adult females; 1 of 4 one-year-old females) lambed (Table 2). Six of the lambs born to adult ewes were born prior to 15 May 2007; the remaining lamb of an adult female was born approximately 23 May. Ewe #50, a 4.5 year-old, was observed with a lamb on the 15 and 16 May; the lamb was not observed again (Appendix 1). The 2 ewes (#34 and #41) that were not observed with lambs in 2005 and 2006 were not observed with lambs in 2007 (Appendix 1). On 2 July 2007, a 1-year-old female (#12) was observed on escape terrain with a nursing lamb. The umbilicus of the lamb, although present, was dry and barely visible; I estimated the lamb to be 1-week-old and later identified it as female. All 7 lambs (5 females, 2 males) that survived to 3 months of age also survived to age 1 year.

Table 2. Lamb production, survival and lamb:ewe ratios of translocated bighorn sheep, in Badlands National Park, South Dakota, USA, in 2005–2007.

<table>
<thead>
<tr>
<th>Year</th>
<th>Lambs &lt; 1 August</th>
<th>Lambs &gt; 1 August</th>
<th>Ewes</th>
<th>Lamb:ewe (&gt; 1.5 years-old)</th>
<th>Rams</th>
<th>Yearling lambs</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>10</td>
<td>9</td>
<td>10</td>
<td>75:100</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>2006</td>
<td>9</td>
<td>8</td>
<td>13</td>
<td>62:100</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>2007*</td>
<td>8</td>
<td>7</td>
<td>13</td>
<td>54:100</td>
<td>9</td>
<td>7</td>
</tr>
</tbody>
</table>

1 Number of lamb observed prior to 1 August, 2 Number of lambs observed after 1 August, 3 Number of females > 2 years old, 4 August lamb:ewe (> 1.5 years-old) ratio, 5 Rams (≥ 1.5 years-old) observed during November of the previous year, 6 Number of lambs surviving from August 1 to 1-year-old,* The lamb of the 1-year-old ewe was included in the lambs observed, but the ewe was not included in the calculation of the lamb:ewe ratio.

Because lambing of a 1-year-old ewe was undocumented, lambing, maternity, and paternity of #12 was determined based on the analysis of 15 microsatellite loci (Chapter 4). Based on the analysis, #12 was the daughter of a 2.5-year-old translocated ewe (i.e.,
#61) and 1.5-year-old translocated male. Ewe #12, born between 23 May and 4 June 2006, was a first generation offspring of the introduction, and was immobilized and radiocollared on 24 May 2007. At capture, ewe #12 appeared healthy and in excellent physical condition, and I was unaware that she was pregnant. Using a 175-day gestation period (Geist 1971), ewe #12 was bred on 2 January 2007 at 212–224 days (≈ 7 months) of age.

**Dispersal**

On 31 May 2006, 9 first-generation offspring born in 2005 to translocated females were observed at BNP within their natal herd range. On 5 June 2006, 6 yearlings (3 females, 3 males) were observed in Wall, South Dakota (Fig. 1) about 15 km north of BNP. Two females (F1, F2) and 1 male (M1) were ear-tagged; remaining individuals (F3, M2, and M3) were not marked. Efforts were made to locate the yearlings over the following weeks but were unsuccessful. I received a report on 17 June 2006 that the 6 yearlings had been observed 121.6 km east of BNP. On 24 June 2006, these bighorns were reported south of Gregory, South Dakota, < 1.6 km from a domestic sheep herd. The bighorn yearlings then separated into 2 groups of 3. Group 1 was comprised of F1, M1, and M2, and group 2 was comprised of F2, F3, and M3. Group 1 was observed twice between 29 June and 11 July 2006 moving from Gregory, South Dakota east to the Missouri River and then north to Lower Brule Sioux Reservation (LBSR). F1 was euthanized on LBSR on 14 July 2006. Based on 14 observations, F1 traveled 417.2 km. Bighorn M1 left LBSR, was observed once and on 27 July 2006 was euthanized near Presho, South Dakota. Based on 17 observations, M1 traveled 524.4 km. Bighorn M2
crossed the Missouri River and was euthanized in Kimball, South Dakota on 16 September 2006. Based on 15 observations, M2 traveled 474.3 km.

After leaving Gregory, South Dakota, group 2 moved south into north-central Nebraska and was observed 3 times. On 9 July 2006, group 2 was observed in a containment pen with domestic goats near Anoka, Nebraska. On 12 July 2006, F2 was euthanized near Butte, Nebraska and based on 11 observations, F2 traveled 340.0 km. M3 was euthanized on 21 July 2006 near Bristow, Nebraska and based on 12 locations,
M3 traveled 366.4 km. F3 was last observed on 12 July 2006 moving east along the Niobrara River in north central Nebraska. Based on 11 locations, F3 traveled 340.0 km.

The remaining 3 yearlings (group 3) included an ear-tagged female (F4), an unmarked female (F5), and 1 unmarked male (M4). Group 3 was observed in BNP on 31 May and was later observed north of Kyle, South Dakota, on the Pine Ridge Reservation on 30 June 2006. Group 3 traveled 43 km based on 2 locations and has not been observed since June 2006 (Table 4).

On 15 May 2007, 8 yearlings born in 2006 to translocated females were observed at BNP within their natal herd range. On 21 May 2007, 3 of the yearling male bighorn sheep were observed north of Quinn, South Dakota, in a pasture with domestic sheep, 25 km northeast of their last location in BNP (Fig. 1). One male was ear-tagged; remaining individuals were not marked. These yearling males were euthanized on 22 May 2007 moving a straightline distance of 25 km.

Necropsy findings

Five of 6 yearlings that dispersed in 2006 were euthanized, necropsied, and tested for disease at the South Dakota Animal Disease Research and Diagnostics Laboratory. Riney’s (1955) kidney fat index ranged from 10.1–18.3% (\(\bar{x} = 14.30\%\)). Adults, non-embryonated eggs, or eggs containing parasitic larvae of the superfamily Protostrongyloidea, were observed through histopathology in 2 females and 1 male. Lungworms had not caused significant clinical disease in the yearling bighorn sheep. Although not identified to genus, lungworms were probably \textit{Protostrongylus} spp. because both \textit{P. stilesi} and \textit{P. rushi} were identified from an adult female in BNP whereas
*Muellerius capillaris* has not been reported (Gamo et al. 1999). Sarcocysts also were observed in cross sections of the heart in 2 females and 1 male; remaining males were not examined for presence of sarcocysts.

All bighorn yearlings tested for border disease (*Pestivirus* spp.), parainfluenza-3 virus (*Paramyxoviridae*), and respiratory syncytial virus (*Paramyxoviridae*) were negative. There were no bacteria isolated from the respiratory tract of 2 males and 1 female. Although *Pasteurella* spp. was isolated from the lungs of 1 yearling male and 1 female, there were no histologic lesions present indicating bronchopneumonia caused by the bacteria.

All 3 yearling males that dispersed in 2007 were euthanized, necropsied, and tested for diseases at the Wyoming State Veterinary Laboratory. Riney’s (1955) kidney fat index ranged from 15.05–20.28% (\( \bar{x} = 19.80\% \)). All individuals tested negative for chlamydia (*Chlamydia* spp.), parainfluenza-3 virus (*Paramyxoviridae*), and bovine respiratory syncytial virus (*Paramyxoviridae*). No significant bacteria were isolated from respiratory tracts, and no histologic lesions indicative of bronchopneumonia or lungworm infection were observed in any individuals.

**DISCUSSION**

Population growth is influenced by 4 factors: reproduction, survival, emigration, and immigration, where number of individuals \( N_t \) at some time \( t \) in the future, can be measured by determining (births-deaths) + (immigration-emigration) (Rockwood 2006). Because emigration and immigration rates are difficult to measure, these rates are typically ignored (i.e., the population is considered to be closed where emigration and
immigration rates = 0) (McCarty and Miller 1998) and population dynamics are assumed to be driven by age- and sex-specific reproduction and survival (McCarty and Miller 1998). Determining these rates (e.g., reproduction and survival) are expensive as it requires capture and collaring of individuals and personnel to vigorously monitor individuals within the population. Therefore, for species such as bighorn sheep, population growth is typically determined through annual population surveys, where information on reproductive and mortality rates can be inferred by determining lamb:ewe ratios and population age structure (Wehausen et al. 1987). These population estimates are inadequate for the evaluation of management strategies as little can be ascertained as to what factors are driving the dynamics of the population (Enk et al. 2001).

Reproductive rate of bighorn sheep is usually determined by calculating lamb:ewe ratios, where a ewe is considered any female >1.5-years-old. This is misleading because reproduction in females is not dependent on the age of a female but rather the amount of time necessary to acquire fat reserves to induce ovulation (Wehausen 1984). It was previously thought that bighorn sheep ewes were unable to acquire adequate fat reserves to induce ovulation (Wehausen 1984) until 2.5 years of age (Buechner 1960, Geist 1971), but production by 1.5-year-old females has recently been accepted as normal in most populations. Berger (1978) suggested that introduced and captive desert bighorn sheep (O. c. nelsoni) may become sexually mature prior to 1 year of age, with early maturation occurring as a function of continuous annual growth (Berger 1982), which would allow minimum body size for reproduction to be achieved at a younger age. Although captive desert bighorn sheep have successfully bred between 9.7 and 10 months of age
(McCutchen 1977, Morgart and Krausman 1983) and it has been suggested that free-ranging desert bighorn sheep can be bred as early as 9.7 months of age (Morgart and Krausman 1983), no observation of this phenomenon has been documented. Production of lambs by < 1 year old females in a free-ranging population of Rocky Mountain bighorn sheep has not been previously reported; therefore, this report represents the first documentation of this rare event.

It has been recommended that transplanted animals be placed in habitats similar to those previously occupied to reduce translocation stress (Douglas and Leslie 1999). Because additional stress may negatively influence reproductive behavior annual lamb:ewe ratios may be the best indicator of the status of an introduced population (Douglas and Leslie 1999). For population increase, 50 lambs:100 ewes are adequate (Lawson and Johnson 1982) but concern is warranted if < 25 lambs:100 ewes are observed during autumn (Douglas and Leslie 1999). Although lamb:ewe ratios decreased from 2004 to 2007, the translocated bighorn sheep population at BNP was considered stable and growing. Decreasing lamb:ewe ratios post-translocation have been observed in other translocated populations in prairie habitat (Lewis 1998). In North Dakota, lamb:ewe ratios of a translocated population of California bighorn sheep decreased from 57:100 to 25:100, with lamb survivorship to 6 months of age estimated at 50% and 100%, respectively, in the 2 years following the translocation (Lewis 1998).

Factors thought to contribute to low lamb:ewe ratios and low survivorship of lambs include poor nutritional condition of ewes, disease, hypothermia, predation, and environmental factors (e.g., precipitation, temperature) (Holl and Bleich 1983, Wehausen
et al. 1987, Hass 1989, Hass 1997, Enk et al. 2001). Although the lamb:ewe ratios of the translocated bighorn sheep at BNP decreased from 2005 to 2007, survivorship of lambs was high (≈ 90%). The decreasing lamb:ewe ratio in BNP may be associated with poor conception rates, fetal mortality, or early post-partum mortality (Shackleton et al. 1999). Maternal condition is more likely to affect early postnatal survival than fetal death (Shackleton et al. 1999), but based on high lamb survival and successful reproduction by 1 and 2-year-old females, I believe that forage quality was not a factor influencing reproductive rates for translocated bighorn sheep during this study.

Low reproductive rates (10–40%) and reduced lamb survival (0–5%) in bighorn sheep also has been attributed to equal ram:ewe ratios resulting in excess ewe harassment by the surplus rams (Fairaizl 1980); however, probability of pregnancy is reduced when the number of rams in the population declines (Lawson and Johnson 1982). Number of rams observed during the rut decreased from 15 in 2004 to 9 in 2005. Of the 9 rams observed in 2005, 6 were 1.5-year-old translocated rams, and 3 were resident rams (2.5-year-old, 4.5-year-old, and 10.5-year-old). No additional rams have been observed with the translocated females since that time. In 2005, the 1.5-year-old rams were observed mounting and chasing translocated ewes and based on paternity analysis (T. J. Zimmerman, South Dakota State University, unpublished data) were successfully reproducing with receptive ewes. Furthermore, translocated rams were present for a longer period of time, pre- and post-rut, compared with resident rams. Although Whiting et al. (2008) recently determined that reproductive rate of bighorn sheep females
was not influenced by ram:ewe ratios or age structure of the ram population, I consider this a hypothesis that requires further investigation.

Proximate causes of mammalian dispersal include competition for mates, competition for resources, or inbreeding avoidance (Greenwood 1980). Bighorn sheep like most other large ungulate species in North America exhibit male-biased dispersal (Geist 1971; Greenwood 1980), although the distance traveled by dispersing bighorn sheep is substantially less compared with other ungulates. Dispersal by young rams is thought to be a function of the pursuit of breeding advantages in ewe groups and is typically observed just prior to or during rut (Geist 1971). Movement of young female bighorn sheep from their natal area is rare because they “adopt the home-ranges of the females that raised them” (Geist 1971). In spring, when pregnant females move to lambing range, yearlings typically are associated with anestrous females, subadults, or adult males (Geist 1971). If these classes of sheep are absent, and yearlings lose contact with adults, they may wander or disperse into unsuitable terrain (Geist 1971). Because dispersal into unfamiliar terrain has the greatest implications for metapopulation dynamics, long-distance movements through unfamiliar or inhospitable habitats may increase an individual’s vulnerability to predation, stress, or malnutrition (Van Vuren 1998), increasing mortality risks and energetic costs (Perrin and Mazalov 1999). Yet, dispersal during seasonal food abundance may have evolved to increase survival, promoting settlement during the most favorable season (Ferreras et al. 2004).

In recent years, biologists in South Dakota have identified noteworthy movements of some large mammals. Thompson and Jenks (2005) reported the longest recorded
dispersal (1,067 km) by a subadult cougar (*Puma concolor*) from South Dakota to Oklahoma, and Kanta and Jenks (unpublished data) reported the longest recorded dispersal of a mountain goat (*Oreamnos americana*) from western South Dakota to western Nebraska. Those dispersals are of particular interest because the individuals were juvenile males that crossed tracts of unsuitable or atypical habitat to complete dispersal movements. Furthermore, Jacques and Jenks (2007) not only reported the longest recorded dispersal distance (267 km) of a yearling male pronghorn (*Antilocapra americana*) but also documented long-dispersal distances (15–41 km) of yearling females in South Dakota. Jacques and Jenks (2007) hypothesized that the long movements of pronghorn were due to fragmentation of sagebrush habitat, requiring greater movements to high-quality habitat.

Reports of northern populations of bighorn sheep dispersing or colonizing new areas are rare (Singer et al. 2000). Bighorn sheep typically avoid densely forested habitats; therefore, northern montane habitats may serve as barriers to range expansion (Geist 1971). The longest documented movement by a Rocky Mountain bighorn sheep male to date was 75 km (Akenson and Akenson 1994). According to Singer et al. (2000), high population growth rates, few water barriers, open vegetation, and rugged terrain in corridors were correlated with successful colonization. Bleich et al. (1996) documented a yearling desert bighorn that emigrated from its natal range, dispersed to a neighboring mountain range, and later produced at least one offspring. Bleich et al. (1996) hypothesized that less conservative dispersal behavior of bighorn sheep may be expected
in areas with sparse vegetation in relatively flat terrain (e.g., desert and prairie ecosystems).

The eastern extent of the bighorn sheep distribution in South Dakota is unclear; therefore, I can only speculate as to whether yearlings dispersed into areas previously occupied by bighorn sheep in South Dakota. Meriwether Lewis and William Clark during their 1804 expedition did not observe bighorn sheep on the Missouri River in present day South Dakota (Coues 1893). Buechner (1960) reported that bighorn sheep range terminated at the badlands and Pine Ridge east of the Black Hills. Yet, according to Cowan (1940), bighorn sheep range included the badlands adjoining the Missouri River in South Dakota. East of BNP, suitable bighorn sheep habitat becomes more fragmented and sparse (Chapter 3).

Dispersing bighorns were euthanized because of contact with domestic sheep and goats. Therefore, it is unknown whether these individuals would have established and successfully bred, returned to their former home-range, or died due to disease. These movements provide more insight into life history and range expansion of bighorn sheep and contribute to the working knowledge of dispersal in mammals.

**LITERATURE CITED**


CHAPTER 2

HOME-RANGE AND HABITAT SELECTION OF TRANSLOCATED AND RESIDENT BIGHORN SHEEP AT BADLANDS NATIONAL PARK, SOUTH DAKOTA
INTRODUCTION

Bighorn sheep (*Ovis canadensis*) are an ecologically fragile species, which were once relatively abundant but now are one of the rarest ungulates in North America (Buechner 1960). Although mountain sheep and humans have coexisted in North America for thousands of years (Hopkins 1967, Hopkins et al. 1982), human impacts in the last 150 years have lead to major declines in bighorn sheep populations (Valdez and Krausman 1999). Bighorn sheep persistence is influenced by the same variables that plague many threatened and endangered species: reduced and fragmented habitat, loss of movement corridors, loss of genetic fitness, disease, competition, predation, and human impacts (Douglas and Leslie 1999). Some of these factors (e.g., overexploitation and diseases of domestic livestock) caused the extirpation of the Audubon’s bighorn ecotype (*Ovis canadensis auduboni* [Merriam 1901] now *O. c. canadensis* [Shaw 1804]), described as a subspecies of bighorn sheep (Cowan 1940). The Audubon’s bighorn inhabited the badlands of the Yellowstone and Missouri rivers in eastern Montana, eastern Wyoming, western North Dakota and South Dakota, and northwestern Nebraska (Valdez and Krausman 1999), with the eastern extent of their range occurring in the South Dakota badlands (Buechener 1960). The last known Audubon’s bighorn in South Dakota was harvested in 1924 or 1925 in Washabaugh (i.e., south Jackson) County, near the present day location of Badlands National Park (BNP).

Management policy of the National Park Service (NPS) is to maintain natural ecosystems and to restore extirpated native flora and fauna if the populations can be self-
perpetuating (National Park Service Management Policy 2006). In an effort to restore bighorn sheep to its former range, the South Dakota Department of Game, Fish and Parks, in conjunction with the NPS released 22 Rocky Mountain bighorn sheep from Pikes Peak, Colorado, into a 150-ha enclosure in BNP in 1964 (Ramey et al. 2000). In 1967, a *Pasteurella* spp. epizootic reduced the population to 14 individuals; surviving individuals were released from captivity. Based on the estimated effective population size and analysis of molecular genetic data, the bighorn sheep population at BNP underwent a population bottleneck at founding (Ramey et al. 2000).

Recommendations to restore genetic diversity of the BNP bighorn sheep populations included a mixed-sex augmentation (*n* > 30) from an outbred, native population of Rocky Mountain bighorn sheep (Ramey et al. 2000). D. M. Shackleton and the International Union for Conservation of Nature and Natural Resources (IUCN)/Species Survival Commission (SCC) Caprinae Specialist Group (1997) also had determined that the ecotypes of bighorn sheep in the mixed-grass badlands were not secure because reserves and protected areas were limited and few of these areas contained bighorn sheep. Thus, conservation measures proposed by the IUCN/SCC were to expand populations and distribution of bighorn sheep throughout their range in the eastern mixed-grass prairie (Shackleton and the IUCN/SCC Caprinae specialist group 1997).

Because of the poor colonizing ability of bighorn sheep, transplant programs have attempted to reestablish populations in localized areas where they have been extirpated or increase population numbers where they have been reduced (Buechner 1960). All
western states in North America have reintroduced populations of bighorn sheep (Shackleton et al. 1999), but the rate of successful establishment of self-sustaining reintroduced populations has been $\approx 50\%$ (Ramey et al. 2000). The outcome of many reintroductions are poorly documented (Gogan 1990), therefore, if introduced sheep were regularly monitored and if each introduction was viewed as an experiment and rigorously evaluated, the rate of successful translocations could increase (Roy and Irby 1994, Douglas and Leslie 1999). Demographic data (e.g., population size, young: adult ratios) may be useful for evaluating success of a reintroduction, providing that information on habitat quantity, quality, and successional trends also are evaluated (Gogan 1990). Much of our knowledge of the ecology of bighorn sheep has been determined through research efforts focused on montane (Geist 1971) and desert populations (Leslie and Douglas 1979). Yet, relatively little is known about low-elevation, non-mountainous bighorn sheep herds that occupy mixed-grass prairie habitats (Fairbanks et al. 1987). Information on home-range size and habitat selection are useful aids for estimating carrying capacity of an ecosystem (Douglas and Leslie 1999). Habitat use studies of reintroduced mammals could provide information into habitat preferences of populations occurring below carrying capacity because individuals would be selecting for optimal habitat conditions (Gogan 1990). If available, these data may assist biologists in meeting the conservation measures proposed by the IUCN/SCC, i.e., to restore and expand populations of bighorn sheep throughout the eastern extent of their range.

The objectives of this study were to: 1) estimate 95% and 50% adaptive kernel, fixed kernel, and minimum convex polygon home-range size of translocated bighorn
sheep, 2) compare 95% and 50% adaptive kernel planimetric and surface area estimates of translocated bighorn sheep home-range size, 2) compare interannual variation in translocated bighorn sheep home-range sizes, and 3) compare home-range size and habitat use of translocated and resident bighorn sheep. I hypothesized that 1) home-range surface area estimates would be larger than planimetric estimates due to terrain ruggedness, 2) home-range size of translocated bighorn sheep would decrease from year 1 to year 2 as proximate resources were identified, and 3) home-range size and habitat selection would differ between translocated and resident bighorn sheep due to the naivety of translocated bighorn sheep to the distribution of resources (Roy and Irby 1994, Owen-Smith 2003) and habituation of the translocated bighorn sheep to humans (Rubin et al. 2002).

**STUDY AREA**

Badlands National Park (Latitude: 43.710880, Longitude: -102.477030) encompasses 98,400 ha and is located in Pennington, Shannon, and Jackson counties within the White River badlands of southwestern South Dakota (Weedon 1999). The badlands of the White River consist of very fine, unconsolidated clay with thin beds of sandstone or isolated concretions (Weedon 1999). Sharp gradients in altitude occur throughout the region with elevation ranging from 700 to 1,000 m above mean sea level (Sweanor et al. 1995). Topography of the badlands was formed because of the coincidence of elevation, rainfall, carving action of streams, and the substrate, resulting in slumps, natural bridges, arches, sod tables, toadstools, and isolated flat remnants of the higher plains (Weedon 1999). These vegetated slumps along with mixed-grass prairie
sod tables occur in close proximity to steep badland terrain and are important feeding areas for bighorn sheep (Gamo et al. 1993). Temperature in the BNP ecosystem ranges from -41 to 47° C, and annual precipitation averages 41 cm (Weedon 1999). Primary roads in BNP are narrow, asphalt based, and 2-lane. Secondary roads are gravel or unimproved dirt that are maintained by BNP. Roadside shoulders along primary and secondary roads are mowed in summer. Potential mammalian predators of bighorn sheep include coyotes (*Canis latrans*), and bobcats (*Felis rufus*). Occasional sign or observations of mountain lions (*Puma concolor*) within the area have been reported, their presence and potential impacts on bighorn sheep in this region are unknown but probably limited. Potential herbivore competitors include bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn antelope (*Antilocapra americana*), and black-tailed prairie dogs (*Cynomys ludovicianus*).

The badlands encompass true short-grass prairie, midgrass prairie, and bunch grass types with plant species including western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), blue grama (*Bouteloua gracilis*), needle and thread grass (*Hesperostipa comata*), fringed sage (*Artemisia frigida*), prairie junegrass (*Koeleria macrantha*), little bluestem (*Schizachyrium scoparium*), green sagewort (*A. ludoviciana*), purple coneflower (*Echinacea angustifolia*), and buffalo grass (*Buchloe dactyloides*) (Weedon 1999). Patches of Rocky Mountain juniper (*Juniperus scopulorum*) and eastern red cedar (*J. virginiana*) occur in upper protected draws and slopes (Weedon 1999). Other species, such as plains cottonwood (*Populus delotoides*), peach-leaved willow (*Salix amygdaloides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and
American elm (*Ulmus americana*), occur in the deciduous complex along the White River (Weedon 1999). Although 42% of BNP is covered by prairie grasslands, over 46% of clay formations on which vegetation is sparse or absent (Von Loh et al. 1999).

**METHODS**

In September 2004, Badlands National Park (BNP) in conjunction with the South Dakota Department of Game, Fish and Parks and the New Mexico Department of Game and Fish, captured 23 (10 adult ewes, 2 yearling ewes, 5 ewe lambs, and 6 ram lambs) Rocky Mountain bighorn sheep at Wheeler Peak in north-central, New Mexico. Bighorn sheep were captured via dropnets and darting (Jessup et al. 1984, Kock et al. 1987). Ewes were aged based on tooth eruption (Taylor 1962) and wear. Adult and yearling ewes were fitted with colored very high frequency (VHF 150–151 MHz) radio transmitters (250 grams and 1.5 lbs—Advanced Telemetry Systems, Isanti, Minnesota). Lambs were marked with numbered red, yellow, or orange ear tags and were later radio-collared. Captured bighorn sheep were released at Conata Basin Picnic Area near Pinnacles in BNP between 24–27 September. Pinnacles was selected as the release site because it had been identified as a site with suitable habitat (Sweanor et al. 1995) and contained a subpopulation comprised of 15 individuals (9 rams, 3 ewes, 1 yearling, and 2 lambs) based on a 2003 ground survey. Capture and handling methods followed recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (1998) and were approved by the South Dakota State University Institutional Animal Care and Use Committee.
Radio-collared females were visually relocated ≥ 3 times weekly from September 2004-2006 using handheld and omni directional antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA). Visual daytime locations (Fairaizl 1980), group composition, and behavior (e.g., feeding, bedded, walking) were recorded. All individuals within the group were identified by radio-collar color, ear tag, or distinguishable markings.

Universal Transverse Mercator (UTM) position of the individual or group was calculated based on the UTM of the observer collected using a handheld GPS, distance to the animal using a Leica© 1200 rangefinder (Leica Camera AG, Solms, Germany) accurate to ± 1m, azimuth using a compass, and the vertical angle of the line of sight using a clinometer.

**Home-range**

To compare home-range size and habitat use of translocated and resident bighorn sheep, I used location data of resident radio-collared females from the Pinnacles subpopulation collected from May 1992 to November 1994 (Gamo et al. 1999, Moses et al. 1996). I entered locations of individual resident and translocated females (Lewis 1998) into a Geographic Information System using UTM datum Zone 13N, NAD83 and converted locations to shapefiles. HOME-RANGE TOOLS ANALYSIS EXTENSION (Rodgers et al. 2005) in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA) was used to calculate 95% and 50% volume contours simultaneously using non parametric adaptive kernel estimators (Worton 1989, Oehler et al. 2003). Default resolution grids and percent volume contours were used and the *ad hoc* bandwidth was created by reducing the reference bandwidth in 10% increments until the 95% contour fractured into ≥ 2 polygons (J. G. Kie, Idaho State University, Pocatello,
Idaho, USA, unpublished data). The *ad hoc* bandwidth was chosen as the bandwidth used just prior to fracturing of the home-range outer contour. Both contours (e.g., 95% and 50%) were determined using the same smoothing parameter. Minimum convex polygons (95%) using a fixed mean were calculated with HOME-RANGE TOOLS ANALYSIS EXTENSION (Rodgers et al. 2005) in ArcGIS 9.2 for comparison with previous studies.

I calculated 3-dimensional (3D) surface area from a digital elevation model (DEM) with 3D Analyst Tools. DEM data (10-m) from BNP were used to create 5-m contour intervals. These contours were used to create triangulated irregular networks (TINs) using the DEM layer for spatial reference. The 95% and 50% adaptive kernel home-range polygons were used to mask the extent of the TIN (Oehler et al. 2005). The 3D Analyst Tool was used to determine the surface area of the home-range polygons using the lowest elevation in the home-range as the reference for statistical analysis.

I performed statistical analysis using SYSTAT (Systat Software Inc., Richmond, California, USA-Wilkinson 1990). Wilcoxon signed-rank tests were used to compare: 1) 95% and 50% adaptive kernel estimates to fixed kernel estimates, 2) interannual home-range size, and 3) planimetric to surface area home-range size. A Kruskal-Wallis test was used to compare planimetric and surface area adaptive kernel home-range sizes between resident and translocated bighorn sheep. Alpha was set at $\leq 0.05$ in statistical analyses.
Habitat Selection

A subset of translocated bighorn sheep \((n = 585)\) locations collected from 29 October 2004 to 28 July 2006 and all locations of resident radio-collared females from the Pinnacles subpopulation collected from May 1992 to November 1994 (Moses et al. 1996, Singer and Gudorf 1999) were added to the GIS. To evaluate habitat selection, the study area was delineated by merging the 95% adaptive kernel home-ranges for resident and translocated bighorn sheep located in the Pinnacles area, and placing a 1,500-m buffer around the polygon. To compare used and available habitat, random points \((n = 1,116)\) located within the study area were generated with the HAWTHS TOOLS extension (Beyer 2004) in ArcGIS 9.2. Random points were distributed throughout the study area. Analyses were contingent on the assumption that locations of the sheep were representative of use in this area and random points were representative of available habitat.

Vegetation (VEG), distance to roads (D2R), distance to wet areas (D2W), slope (SL), and distance to escape terrain (D2ET) have been identified as critical components of bighorn sheep habitat (Valdez and Krausman 1999). Model sets were created, a priori, based on biologically reasonable combinations of variables and used to compare locations of translocated and resident bighorn sheep.

I converted the vegetation shapefile for BNP (Von Loh et al. 1999) to a raster, and reclassified the 32 vegetation associations into 6 major vegetation types: grasslands (GR), shrublands (SH), human-use areas (HU), wet areas (WA), woodlands (WO), and
unvegetated badlands (BA) (Table 3). Each vegetation type was assigned a value from 0 to 5. Unvegetated badlands were used as the categorical reference in the model.

Table 3. Area of reclassified vegetation types at Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Area (km$^2$)</th>
<th>% of Study Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>99.23</td>
<td>62.8</td>
</tr>
<tr>
<td>Shrubland</td>
<td>1.78</td>
<td>1.1</td>
</tr>
<tr>
<td>Human-use</td>
<td>0.63</td>
<td>0.4</td>
</tr>
<tr>
<td>Wet Areas</td>
<td>2.18</td>
<td>1.4</td>
</tr>
<tr>
<td>Woodlands</td>
<td>0.99</td>
<td>0.6</td>
</tr>
<tr>
<td>Badlands*</td>
<td>53.17</td>
<td>33.7</td>
</tr>
<tr>
<td>Total</td>
<td>157.97</td>
<td>100</td>
</tr>
</tbody>
</table>

* Categorical reference

Road shapefiles of Pennington, Jackson, and Shannon counties from the South Dakota Department of Transportation were merged and converted to a raster coverage. Straight-line distances to roads, wet areas, and escape terrain were calculated using SPATIAL ANALYST in ArcGIS 9.2. Distance variables were calculated in kilometers for ease of interpretation. Slope values calculated in degrees were determined from a 10-m DEM of the study area with the SPATIAL ANALYST extension in ArcGIS 9.2. Escape terrain was defined as slopes $\geq 40^\circ$ (Chapter 3).

I attached the value from the raster data to the point data (Russell 2006) using the intersect point tool from HAWTHS TOOLS extension in ArcGIS 9.2. Tukey’s HSD was used to compare point data from independent variables (e.g., D2R, D2W, SL, and D2ET) among random, translocated, and resident bighorn sheep locations. Point data from independent (e.g., D2ET, D2W, D2R, SL) and categorical (e.g., VEG) variables were incorporated into the model. Correlation matrices were examined to detect
multicollinearity. Model fit was assessed using a Hosmer-Lemeshow test using 10 bins with equal counts per bin (Hosmer and Lemeshow 2000). Logistic regression was performed (Manly et al. 2002) to determine the best model for predicting habitat selection of resident and translocated bighorn sheep (Schoenecker 2004). Dichotomous response variables were 1) translocated bighorn sheep locations and 2) resident bighorn sheep locations. To compare models within a model set, Akaike's Information Criterion for small sample sizes (AICc) was used (Burnham and Anderson 2002). Because McFadden's rho-squared (MR²) is intended to mimic r² (Steinberg and Colla 1999), it was used to compare models within model sets and to assess model performance. Following Hensher and Johnson (1981), MR² values between 0.20 and 0.40 were considered satisfactory. Resource Selection Probability Functions (RSPF) were calculated for highly supported models by transforming the logit \( g(x) = \beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p \) using the following equation from Manly et al. (2002):

\[
RSFP = w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p)}
\]

where \( \beta_0, \ldots, \beta_p \) were the parameter estimates and \( x_1, \ldots, x_p \) were the habitat variable values (van Manen and Pelton 1997, Schoenecher 2004). The ratio of sampling probabilities were not estimated, and thus, RSPF represented an index of selectivity (Manly et al. 2002). The raster calculator in ArcGIS 9.2 was used to map RSPF estimates. Categories classified by Schoenecher (2004) were used to define habitat suitability: suitable (0.75 ≤
probability of use $\leq 1.0$), acceptable ($0.50 \leq$ probability of use $< 0.75$), marginal ($0.25 \leq$ probability of use $< 0.50$), and unsuitable ($0.00 \leq$ probability of use $< 0.25$).

RESULTS

Home-range

From 24 September to 28 October 2004, translocated bighorn sheep moved from the release site to the area where they established permanent home-ranges; locations collected between these dates were not used in home-range analyses. Locations collected from 29 October 2004 to 28 July 2006 were used to calculate total home-range size, locations collected from 28 October 2004 to 28 July 2005 were considered year 1 data, and locations collected from 29 October 2005 to 28 July 2006 were considered year 2. Number of locations, 95% and 50% adaptive and fixed home-range size, and h-ref values for individual resident and translocated bighorn sheep are reported in Appendix 2–5.

The 95% adaptive kernel home-range estimate ($\bar{x} = 15.5; \text{SE} = 1.3$) and the 95% fixed kernel home-range estimate ($\bar{x} = 16.1; \text{SE} = 1.3$) for the translocated bighorn sheep did not differ ($Z = 1.664, \ P = 0.096$). The 95% adaptive kernel home-range estimate and the MCP estimate ($\bar{x} = 16.3; \text{SE} = 1.0$) did not differ ($Z = 1.250, \ P = 0.211$). Although there were no statistical differences between the size of the 95% adaptive kernel and MCP home-range estimates, MCP included lands not known to be used by bighorn sheep (Fig. 2). The 50% fixed kernel home-range estimate ($\bar{x} = 3.1; \text{SE} = 0.3$) was greater ($Z = 3.410, \ P = 0.001$) than the 50% adaptive kernel home-range estimate ($\bar{x} = 1.8; \text{SE} = 0.1$).
Figure 2. Comparison of adaptive kernel home-range estimate (A) and minimum convex polygon home-range estimate (B) of a translocated bighorn sheep female from Badlands National Park, South Dakota, USA, in 2004–2006.

The 95% adaptive kernel planimetric and 3D surface area estimates were greater in year 1 compared with year 2 ($Z = -2.691, P = 0.007; Z = -2.691, P = 0.007$, respectively), but the 50% adaptive kernel and surface area estimates did not differ ($Z = -0.756, P = 0.450; Z = -0.890, P = 0.373$, respectively) between years (Table 4).

The 95% and 50% 3D surface areas of translocated sheep were greater than the 2D planimetric area ($Z = 3.408, P = 0.001; Z = 3.408, P = 0.001$, respectively) (Table 4). In year 1, the 95% and 50% surface areas also were greater than planimetric area in year 1 ($Z = 3.200, P = 0.001; Z = 3.113, P = 0.002$, respectively). In year 2, the 95% and 50% surface areas were greater than planimetric area ($Z = 3.200, P = 0.001; Z = 3.256, P = 0.001$, respectively). The 95% and 50% surface areas estimate of the resident bighorns
were greater than planimetric area ($Z = 2.207, P = 0.027; Z = 2.207, P = 0.027$, respectively (Table 4).

The 95% and 50% adaptive kernel estimates were greater in resident than translocated sheep ($U = 6.00, P = 0.002; U = 5.00, P = 0.002$, respectively) (Table 4). The 95% and 50% surface areas also were greater in resident than translocated sheep ($U = 6.000, P = 0.002; U = 4.500, P = 0.002$, respectively) (Table 4).

**Habitat selection**

Distance to water, D2R, and slope differed ($P < 0.05$) between random points, resident bighorn sheep locations, and translocated bighorn sheep locations (Table 5). Translocated bighorn sheep locations were on more vertical slopes ($P < 0.001$) (Table 5, Fig. 3A), closer to wet areas ($P < 0.001$) (Table 5, Fig. 3B), closer to roads ($P < 0.001$) (Table 5, Fig. 3C), and closer to escape terrain ($P < 0.001$) (Table 5, Fig. 3D) compared with random locations. Resident bighorn sheep locations were on more vertical slopes ($P < 0.001$) (Table 5, Fig. 3A), closer to wet areas ($P < 0.001$) (Table 5, Fig.

<table>
<thead>
<tr>
<th>Model</th>
<th>Resident</th>
<th>Translocated</th>
<th>Year 1</th>
<th>Year 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adaptive</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95%</td>
<td>31.3 (3.5)</td>
<td>15.5 (1.3)</td>
<td>18.3 (1.2)</td>
<td>14.4 (1.2)</td>
</tr>
<tr>
<td>50%</td>
<td>3.9 (0.5)</td>
<td>1.8 (0.1)</td>
<td>2.0 (0.1)</td>
<td>1.9 (0.1)</td>
</tr>
<tr>
<td>Surface Area</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95%</td>
<td>33.0 (3.6)</td>
<td>16.0 (1.4)</td>
<td>18.9 (1.3)</td>
<td>15.0 (1.2)</td>
</tr>
<tr>
<td>50%</td>
<td>4.2 (0.5)</td>
<td>1.9 (0.1)</td>
<td>2.1 (0.1)</td>
<td>2.0 (0.1)</td>
</tr>
<tr>
<td>MCP</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>95%</td>
<td>18.1 (1.4)</td>
<td>16.6 (1.2)</td>
<td>16.1 (1.1)</td>
<td>11.4 (0.3)</td>
</tr>
</tbody>
</table>
Table 5. Tukey’s HSD comparison of habitat variables at random points, resident bighorn sheep locations (1992–1994), and translocated bighorn sheep locations (2004–2006) in Badlands National Park, South Dakota, USA. Different letters indicate significant differences ($P < 0.05$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Random</th>
<th>Resident</th>
<th>Translocated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope (°)</td>
<td>6.38 (0.28) A</td>
<td>16.37 (0.52) B</td>
<td>10.82 (0.40) C</td>
</tr>
<tr>
<td>Distance to water (km)</td>
<td>0.44 (0.01) A</td>
<td>0.60 (0.02) B</td>
<td>0.36 (0.01) C</td>
</tr>
<tr>
<td>Distance to roads (km)</td>
<td>1.50 (0.03) A</td>
<td>1.39 (0.04) B</td>
<td>0.23 (0.01) C</td>
</tr>
<tr>
<td>Distance to ET (km)</td>
<td>0.78 (0.02) A</td>
<td>0.11 (0.01) B</td>
<td>0.13 (0.01) B</td>
</tr>
</tbody>
</table>

Figure 3. Comparison of least squares means of slope (A), distance to water (B), distance to roads (C), and distance to escape terrain (D) least squares means between random points, resident bighorn sheep locations (1992–1994), and introduced bighorn sheep locations (2004–2006) at Badlands National Park, South Dakota, USA.
closer to roads \( P = 0.041 \) (Table 5, Fig. 3C), and closer to escape terrain \( P < 0.001 \) (Table 5, Fig. 3D) compared with random locations. Translocated bighorn sheep were on more \( P < 0.001 \) horizontal slopes (Table 5, Fig. 3A), closer to wet areas \( P < 0.001 \) (Table 5, Fig. 4), and closer to roads \( P < 0.001 \) (Table 5, Fig. 5) compared with resident bighorn sheep. Translocated and resident bighorn sheep locations did not differ \( P = 0.800 \) in their proximity to escape terrain (Table 5, Fig. 6).

Based on \( MR^2 \) and Akaike weights, the best model was the full model (Table 6). This model included the continuous variables D2ET, SL, D2R, and the categorical variable VEG. Although the \( MR^2 \) value was high, the final model had poor fit (Hosmer-

Figure 4. Comparison of resident (1992–1994) and introduced (2004–2006) bighorn sheep locations and their proximity to wet areas at Badlands National Park, South Dakota, USA.
Figure 5. Comparison of resident (1992–1994) and introduced (2004–2006) and their proximity to roads at Badlands National Park, South Dakota, USA.

Figure 6. Comparison of resident (1992–1994) and introduced (2004–2006) bighorn sheep locations and their proximity to escape terrain (i.e., slopes ≥ 40°) at Badlands National Park, South Dakota, USA.
Lemeshow \( P = 0.001, \text{df} = 8 \). Based on the odds ratios, translocated bighorns occupied areas further from slopes \( \geq 40^\circ \), on more horizontal slopes, closer to roads, and closer to wet areas than resident bighorn sheep (Table 7). Translocated and resident bighorn sheep


<table>
<thead>
<tr>
<th>#</th>
<th>( w_i )</th>
<th>Model</th>
<th>( ^2 \text{AICc} )</th>
<th>( ^3 \Delta \text{AICc} )</th>
<th>( ^4 \text{K} )</th>
<th>( ^4 \text{MR}^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.84</td>
<td>( 3.33 + 2.30 (D2ET) - 0.04 (SL) -2.82 (D2R) + 0.16 (GR) - 1.10 (SH) + 1.35 (HU) - 0.39 (WA) - 1.04 (WO) - 2.47 (D2W) )</td>
<td>806.95</td>
<td>0</td>
<td>11</td>
<td>0.52</td>
</tr>
<tr>
<td>2</td>
<td>0.16</td>
<td>( 3.37 + 2.57 (D2ET) - 2.92 (D2R) - 0.04 (SL) - 2.39 (D2W) )</td>
<td>810.27</td>
<td>3.32</td>
<td>6</td>
<td>0.51</td>
</tr>
<tr>
<td>3</td>
<td>0.00</td>
<td>( 2.49 + 3.55 (D2ET) - 2.78 (D2R) - 2.53 (D2W) + 0.54 (GR) - 0.79 (SH) + 1.66 (HU) - 0.35 (WA) - 0.87 (WO) )</td>
<td>821.49</td>
<td>14.54</td>
<td>10</td>
<td>0.51</td>
</tr>
<tr>
<td>4</td>
<td>0.00</td>
<td>( 2.62 + 4.74 (D2ET) - 2.96 (D2R) - 2.54 (D2W) )</td>
<td>831.85</td>
<td>24.91</td>
<td>5</td>
<td>0.49</td>
</tr>
<tr>
<td>5</td>
<td>0.00</td>
<td>( 2.17 + 3.81 (D2ET) - 3.09 (D2R) - 0.05 (SL) )</td>
<td>885.03</td>
<td>78.08</td>
<td>5</td>
<td>0.46</td>
</tr>
<tr>
<td>6</td>
<td>0.00</td>
<td>( 1.11 - 3.19 (D2R) + 7.49 (D2ET) )</td>
<td>920.69</td>
<td>113.74</td>
<td>4</td>
<td>0.44</td>
</tr>
<tr>
<td>7</td>
<td>0.00</td>
<td>( 1.08 - 2.70 (D2ET) - 2.60 (D2R) + 1.23 (GR) + 0.90 (SH) + 4.04 (HU) + 1.06 (WA) - 1.32 (WO) )</td>
<td>1306.19</td>
<td>499.24</td>
<td>9</td>
<td>0.21</td>
</tr>
<tr>
<td>8</td>
<td>0.00</td>
<td>( -0.46 + 1.41 (GR) + 1.82 (SH) + 4.07 (HU) + 1.59 (WA) - 0.94 (WO)-0.81 (D2ET) )</td>
<td>1429.35</td>
<td>622.41</td>
<td>8</td>
<td>0.13</td>
</tr>
<tr>
<td>9</td>
<td>0.00</td>
<td>( -0.53 + 1.34 (GR) + 1.83(SH)+3.97 (HU) + 1.23 (WA) - 0.99 (WO) )</td>
<td>1428.99</td>
<td>622.05</td>
<td>7</td>
<td>0.13</td>
</tr>
<tr>
<td>10</td>
<td>0.00</td>
<td>( 0.73 - 0.05 (SL) - 0.66 (D2ET) )</td>
<td>1557.41</td>
<td>750.46</td>
<td>4</td>
<td>0.05</td>
</tr>
<tr>
<td>11</td>
<td>0.00</td>
<td>( 0.61 - 0.05 (SL) )</td>
<td>1556.76</td>
<td>749.81</td>
<td>3</td>
<td>0.04</td>
</tr>
<tr>
<td>12</td>
<td>0.00</td>
<td>( -0.17 + 1.37 (D2ET) )</td>
<td>1620.90</td>
<td>813.96</td>
<td>3</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^1 \text{wi} = \text{Akaike weights}, \quad ^2 \text{AICc} = \text{Akaike's Information Criterion for small sample sizes}, \quad ^3 \text{K} = \text{number of parameters}, \quad ^4 \text{MR}^2 = \text{McFadden's rho-squared}, \quad \text{D2ET} = \text{Distance to slopes} > 40, \quad \text{D2R} = \text{Distance to road}, \quad \text{D2W} = \text{Distance to wet areas}, \quad \text{GR} = \text{Grasslands}, \quad \text{SH} = \text{Shrublands}, \quad \text{HU} = \text{Human-use areas}, \quad \text{WA} = \text{Wet areas}, \quad \text{WO} = \text{Woodlands}.\)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Odds Ratio</th>
<th>95% CI Upper</th>
<th>Lower</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>D2ET</td>
<td>10.014</td>
<td>77.564</td>
<td>1.293</td>
<td>Translocated bighorns were 10 × more likely than resident bighorns to inhabit an area 1 km from 40° slopes than a location adjacent to 40° slopes</td>
</tr>
<tr>
<td>SL</td>
<td>0.961</td>
<td>0.980</td>
<td>0.943</td>
<td>Translocated bighorns were 1 × less likely compared with the resident bighorns to inhabit an area with a 1° increase in the slope</td>
</tr>
<tr>
<td>D2RS</td>
<td>0.060</td>
<td>0.086</td>
<td>0.042</td>
<td>Translocated bighorns were 17 × less likely compared with the resident bighorns to inhabit an area 1 km from a road than a location adjacent to a road</td>
</tr>
<tr>
<td>D2W</td>
<td>0.084</td>
<td>0.152</td>
<td>0.047</td>
<td>Translocated bighorns were 13 × less likely compared with the resident bighorns to inhabit an area 1 km from a wet area than a location adjacent to a wet area</td>
</tr>
<tr>
<td>GR</td>
<td>1.173</td>
<td>1.876</td>
<td>0.734</td>
<td>Translocated bighorns were as likely as resident bighorns to inhabit grasslands as badlands</td>
</tr>
<tr>
<td>SH</td>
<td>0.332</td>
<td>1.314</td>
<td>0.084</td>
<td>Translocated bighorns were as likely as resident bighorns to inhabit shrublands as badlands</td>
</tr>
<tr>
<td>HU</td>
<td>3.843</td>
<td>17.634</td>
<td>0.837</td>
<td>Translocated bighorns were as likely as resident bighorns to inhabit human-use areas as badlands</td>
</tr>
<tr>
<td>WA</td>
<td>0.676</td>
<td>93.964</td>
<td>0.005</td>
<td>Translocated bighorns were as likely as resident bighorns to inhabit water areas as badlands</td>
</tr>
<tr>
<td>WO</td>
<td>0.353</td>
<td>0.851</td>
<td>0.147</td>
<td>Translocated bighorns were 3 × less likely as resident bighorns to inhabit woodlands as badlands</td>
</tr>
</tbody>
</table>

D2ET = Distance to slopes > 40, D2R = Distance to road, D2W = Distance to wet areas, GR = Grasslands, SH = Shrublands, HU = Human-use areas, WA = Wet areas, WO = Woodlands, SL = Slope.
were as likely to select grasslands, shrublands, human-use areas, and wet areas as the categorical reference badlands; however, translocated bighorn sheep were $3 \times$ less likely than resident bighorn sheep to inhabit woodlands as they were badlands (Table 7).

**DISCUSSION**

Determining size, distribution, and quality of habitat patches are useful aids in estimating the number of animals an area can support (Douglas and Leslie 1999). Therefore, the aim of home-range analysis should be to use the estimator that most accurately represents the use of the individual or population. Studies of bighorn sheep have used MCP to estimate home-range size (Leslie and Douglas 1979) yet kernel estimators provide a more accurate means of estimating home-range size compared with MCP (Blundell et al. 2001). Home-range estimates using adaptive or fixed kernel techniques have been applied to many montane species. Nevertheless, there is a paucity of information on home-range size of Rocky Mountain bighorn sheep using adaptive kernel techniques (Shackleton et al. 1999). The only published kernel estimate of bighorn sheep home-range size was provided by Oehler et al. (2003). Adaptive kernel home-range sizes of translocated and resident bighorn sheep at BNP were smaller than the 95% (34.5–65.98 km$^2$) and 50% (5.14–10.01 km$^2$) adaptive kernel home-range area of Nelson’s bighorn ($O. c. nelsoni$) females (Oehler et al. 2003). Larger home-range sizes of desert compared with northern bighorn subspecies may be expected due to more widely distributed resources in desert ecosystems (Oehler et al. 2003).

Escape terrain (e.g., steep slopes, rocky outcrops) is one of the most critical habitat attributes for bighorn sheep ewes, with individuals located within 100–300 m of
these areas (Smith et al. 1991, Sweanor et al. 1995, Douglas and Leslie 1999). At BNP, resident and translocated bighorn sheep were, on average, < 150 m from escape terrain, resulting in linear home-ranges that were closely associated with badland formations. Species associated with geographical features on the landscape (e.g., river otters \textit{[Lutra canadensis]}, caribou \textit{[Rangifer tarrandus]}) tend to have linear home-ranges (Blundell et al. 2001, Maier et al. 1998). Use of minimum convex polygons for linear home-ranges typically results in the inclusion of large expanses of land not used by the animal, which results in overestimation of home-range size (Blundell et al. 2001). Although I found no statistical differences in home-range size between estimators, my data supports others (Worton 1989, Seaman et al. 1999) who concluded that kernel estimators provide a more accurate representation of areas used by species compared with those of minimum convex polygons.

Home-range size is usually presented based on planimetric area and therefore does not account for the true surface area traversed by the animal (Jenness 2004). For species that are associated with topographic ruggedness, such as bighorn sheep and mountain goats \textit{(Oreamnos americana)}, planimetric home-range size underestimates the actual spatial requirements of the animal. According to my analysis, surface area estimates of bighorn sheep home-ranges were larger than planimetric estimates indicating that the area required by bighorn sheep is larger than previously expected. Scientists attempt to make comparisons of home-range size between populations without accounting for elevation relief and ruggedness of the terrain within the home-range. Little regard is given to the fact that a planimetric home-range of 2 km² in the mountains
has a much larger surface area than a 2 km² planimetric home-range in the prairie. Sweanor et al. (1995) estimated carrying capacity of bighorn sheep in the greater BNP ecosystem by determining the total area of suitable bighorn sheep habitat divided by average home-range size. Consideration was not given to the variability in topographic ruggedness found throughout the greater BNP ecosystem. Surface area, in contrast to planimetric area, provides a more useful estimate of the land available for an animal (Jenness 2004). As the slope of terrain fluctuates throughout an individual’s home-range so does the surface area traversed by the animal (Stone et al. 1997). Research by Dailey and Hobbs (1989) demonstrated that energy expenditures (J/ (kg·m)) for bighorn sheep doubled when angle of walking increased from 3.5° to 21.5° while efficiency decreased by 26.6 %. Therefore, energy costs of locomotion in steep terrain may be important factors contributing to distribution and abundance of bighorn sheep (Dailey and Hobbs 1989).

Although independence of locations is usually a major consideration in calculating home-range (Swihart and Slade 1985), Blundell et al. (2001) determined that autocorrelation of locations had no effect on kernel estimates of linear home-ranges. For gregarious species such as bighorn sheep, the rules of independence are often violated because the location of an individual may be influenced by the presence of other sheep. For these reasons, home-range size is usually calculated for the herd and not the individual (Festa-Bianchet 1986). When bighorn sheep are captured for translocation, relatedness, group association, and social status of individuals may be unknown, especially if range use by ewe groups overlap and group mixing occurs at trapping
locations (Festa-Bianchet 1986). Festa-Bianchet (1986) proposed that bighorn sheep females can recognize group conspecifics and therefore may not permanently join other groups. Group fidelity may influence the social organization of translocated bighorn sheep (Roy and Irby 1994); therefore, calculating individual home-range size vs. herd home-range size may be more appropriate for translocated bighorn sheep whose group origin and association are unknown. There was variability (11.1–28.6 km²) in individual home-range sizes of translocated bighorn sheep at BNP, and no clear pattern was evident to describe the variability that was identified in this population. Within herd variability of home-range size has been observed in other populations, but ultimate cause of variation has not been identified (Oehler et al. 2005). Due to this variability, I believe that the mean of the individual home-ranges provided a better measure of the area utilized by conspecifics than the herd home-range size estimates.

Emphasis should be placed on the core of the animals’ home-range for comparative purposes such as home-range size between populations, measures of overlap, and inter- or intra-annual variation (Seaman et al. 1999). In some studies, the area used by translocated populations of bighorn sheep gradually increases over time (Lewis 1998, Roy and Irby 1994). Although I observed no interannual variation in the core area of use, the 95% kernel home-range size decreased from year 1 to year 2. Initially the population may have surveyed the landscape to identify the spatial distribution of resources needed. After these resources had been identified, they could select the optimal sites where needs for survival and reproduction were met (Owen-Smith 2003).
Habitat suitability is dependent on adequate food resources balanced with the needs of predator avoidance and adequate shelter from environmental conditions (Owen-Smith 2003). According to Owen-Smith (2003), reproductive success and population growth rates of introduced ungulates are often poor in the first few years following release but over time these parameters increase. He suggested that this pattern may be associated with decreasing physiological condition in response to the time required by the introduced animals to identify new suitable forages and their distribution throughout the landscape. This pattern may be curtailed if translocated populations intermingle with resident populations to learn habitat-use patterns. Although intermingling of a translocated and resident bighorn sheep herd in North Dakota was observed within the first 2 years following a translocation (Lewis 1999), I did not observe social integration during this study. At the population level, lack of social integration may have benefits. Roy and Irby (1994) reported that because social integration did not occur, transplanted bighorns occupied areas not regularly used by resident sheep, increasing occupied bighorn sheep habitat by 32%.

Bighorn sheep typically avoid densely forested habitats to circumvent predators (Geist 1971). It has been recommended that transplanted animals be placed in habitats they are adapted to and thus, similar to the original occupied area (Douglas and Leslie 1999). Translocated bighorn sheep at BNP were removed from an alpine ecosystem in north-central New Mexico where an established population of mountain lions existed (E. Rominger, New Mexico Department of Game and Fish, personal communication). Large predators (e.g., wolves [Canis lupus], mountain lions) of bighorn sheep have been
extirpated or severely reduced throughout the BNP ecosystem. Resident bighorns at BNP may have adapted to a “predator free” system, and used areas with dense vegetation (e.g., juniper woodlands), whereas translocated bighorn sheep avoided densely vegetated areas. Selection of coniferous stands by bighorn sheep also could provide a thermoregulatory advantage (Fairbanks et al. 1987, Schoenecher 2004). The thermal neutral zone of bighorn sheep is -20–20° C (Chappel and Hudson 1978). If temperature decreases from –20° C to –30° C, there is a 37 to 39% increase in the metabolic rate of bighorn sheep, and if winds exceed 8 m/sec when temperatures are < –20° C, additional increases in metabolic costs may occur (Chappel and Hudson 1978). Fairbanks et al. (1987) speculated that preference of conifer forests by bighorn sheep in northwestern Nebraska may have been for thermal regulation in winter; therefore, selection of juniper patches by bighorn sheep in BNP may serve a similar thermoregulatory function. At BNP, bighorn sheep may be exposed more to the upper threshold of their thermal neutral zone due to the hot climate; therefore, woodlands may be sought as a source of shade during the summer. Further analysis of seasonal habitat selection may provide more insight into habitat requirements of bighorn sheep at BNP.

Perennial water sources need to be within 3.2 km of core areas used by bighorn sheep (Smith et al. 1991). Based on areas identified from the vegetation shapefile for BNP (Von Loh et al. 1999), water availability was not a limiting factor for bighorn sheep at BNP as all bighorn sheep locations were within 2 km of wet areas. Temporary and permanent water sources at BNP could not be distinguished through GIS; therefore, the extent of the availability of permanent water sources to bighorn sheep at BNP may be
limited. Due to the high clay content of soils within BNP, precipitation is temporarily retained in small pools in shaded stream beds. These small pools may serve as additional sources of water, but the duration of water retention, extent of availability, and use of these pools by bighorn sheep and other wildlife is unknown. Locations of translocated bighorns at BNP were located farther from 40° slopes and closer to wet areas compared with resident bighorn sheep locations. These 2 habitat variables were probably inversely correlated as flatter areas were more likely to contain springs and reservoirs compared with steep areas. Areas typically used by resident bighorn sheep appeared to have a greater availability of slopes ≥ 40° than the area selected by translocated bighorn sheep; therefore, locations of resident bighorn sheep were inherently closer to steep slopes. The closer proximity of resident bighorn sheep to escape terrain also may have been biased by visual relocation as resident bighorns at BNP typically flee to escape terrain when approached by humans.

Bighorn sheep populations and individuals within the populations are vary in their response to anthropogenic activities (Geist 1975, Papouchis et al. 2001). Papouchis et al. (2001) determined that desert bighorn sheep avoided hikers more than vehicular traffic, and fleeing response decreased with increasing proximity to escape. Pelletier (2006) determined that bighorn sheep behavior was not influenced by high traffic volume, whereas mule deer and white-tailed deer used alternative habitats during times of high traffic volume. Therefore, tolerance of roads and anthropogenic activities may be advantageous to reduce interspecific and intraspecific competition. Translocated bighorn sheep at BNP selected habitats near roads, whereas resident bighorn sheep avoided areas
with roads. I examined distributions of locations within 10 and 50 m of a road and approximately 10% of the translocated bighorn locations were within 10 m of a road compared with 0.3% of the resident locations; approximately 30% of the translocated bighorns locations occurred within 50 m of a road compared with 4% of the resident locations.

I postulate that there may be multiple reasons to explain selection for roads by the translocated bighorn sheep. First, the translocated bighorn sheep were acclimated to the presence of humans in their former range increasing their tolerance of human activities in BNP (E. Rominger, New Mexico Department of Game and Fish, personal communication). I speculate that when the bighorn sheep were released, they exploited habitat where resources were proximately located. The bighorn sheep selected an area with roads and high human-use, where resource richness may have outweighed the trade-offs associated with predation risk (i.e., human-caused disturbance stimuli); (Frid and Dill 2002). Secondly, because of substrate disturbance in road side areas, exotic flora richness may be greater compared with undisturbed sites (Tyser and Worley 1992). Exotic forb species may have a higher protein content compared with native forbs and availability may occur during periods when native forbs are limited (Rubin et al. 2002). Rubin et al. (2002) reported smaller core home-ranges, use of less steep slopes, higher fecal nitrogen values, and greater diet composition of non-native plants in a population of bighorn sheep using an urban environment compared with a non-urban population. Although diet quality and quantity were not measured, I observed smaller home-ranges and use of less steep slopes by translocated bighorn sheep occupying high human-use
areas compared with resident bighorn sheep that were established farther from human-use areas.

The use of areas with high anthropogenic use also may have deleterious effects on population parameters because true habituation to anthropogenic disturbance is often partial or negligible (Bleich et al. 1994, Frid and Dill 2002). Excessive harassment and chase of bighorn sheep by humans increases energy expenditure by 20–1,500% above standing (Geist 1975). Research also has indicated that bighorn sheep were more fearful of domestic dogs than coyotes, eliciting an escape distance of 108.3–130 m (Pelletier 2006). The reaction of bighorn sheep to domestic dogs occurred regardless of whether the dog was free ranging or leashed (Pelletier 2006). High energy expenditures may cause a decline in population parameters (e.g., survival, reproduction), growth rates, horn size, and overall health (Geist 1975, Frid and Dill 2002). In National Parks such as BNP, bighorn sheep need to be managed not only for their intrinsic value but also for nonconsumptive uses (e.g., photography, education, aesthetics). Geist (1975) recommended that bighorns occupying these ranges need to be habituated to human presence and that humans frequenting bighorn sheep ranges need to be educated in tactful behavior around bighorn sheep and other wildlife species. If disturbance stimuli are long term or intensive, shifts to lower quality habitat or reduced access to resources may occur in efforts to avoid disturbance stimuli (Papouchis et al. 2001, Frid and Dill 2002) and in some cases recreational activity may cause bighorn sheep to vacate suitable habitat (Papouchis et al. 2001).
LITERATURE CITED


Steinberg, D., and P. Colla. 1999. Logistic regression in SYSTAT 9 Statistics I. SPSS. USA.


CHAPTER 3

BIGHORN SHEEP HABITAT MODELS FOR BADLANDS NATIONAL PARK
AND WESTERN SOUTH DAKOTA
INTRODUCTION

Prairie ecosystems differ from montane systems inhabited by most well-studied bighorn sheep populations (Fairbanks et al. 1987, Moses et al. 1996); therefore, characteristics identified as critical features in mountain ecosystems may not be important to prairie bighorn sheep populations. Smith et al. (1991) developed a habitat evaluation procedure (HEP) to identify bighorn sheep habitat in the Intermountain West. The HEP incorporated the parameters escape terrain, a buffer surrounding escape terrain, proximity to water sources, natural barriers, man-made barriers, horizontal visibility, human-use areas, and proximity to domestic livestock (Smith et al. 1991). Parameters used in the HEP were derived from data collected from montane populations of bighorn sheep (Smith et al. 1991, Schoenecker 2004). Although little is known about habitat requirements or preferences of bighorn sheep occupying low-elevation prairie ecosystems (but see Fairbanks 1987, Moses et al. 1996, Lewis 1998), the parameters identified in the intermountain HEP have been applied to identify suitable habitat in prairie ecosystems (Gudorf et al. 1994, Sweanor et al. 1995).

Sweanor et al. (1995) utilized a modified HEP developed by Smith et al. (1991) to determine suitable habitat for bighorn sheep at Badlands National Park (BNP). The model was created using 30-m and 90-m Digital Elevation Model and Defense Mapping Agency data. In the model, suitable bighorn sheep habitat included a 300-m buffer around slopes between 27° and 85°, and areas ≤ 1,000-m wide that were bounded on ≥ 2 sides by slopes >27°. Sweanor et al. (1995) determined that other variables (e.g., horizontal visibility, water sources, natural barriers, human-use areas, man-made barriers,
domestic livestock) deemed important by Smith et al. (1991) were not limiting factors for the bighorn sheep distribution at BNP. Sweanor et al. (1995) determined that 802 km$^2$ of the 5,322 km$^2$ study area was suitable bighorn sheep habitat and that escape terrain was the dominant variable affecting amount of suitable habitat. Using forage biomass estimates from the North Dakota badlands and the results from the modified Smith et al. (1991) model, they determined that 400–600 bighorn sheep could be sustained in the greater BNP ecosystem. Due to the ruggedness of the badlands, Zimmerman et al. (2006) reevaluated the Sweanor et al. (1995) model utilizing the same parameters but with 10-m digital elevation model (DEM) data. Zimmerman et al. (2006) determined that a finer DEM resolution increased the amount of suitable bighorn sheep habitat by 2.5 times, increasing the amount of suitable habitat in the greater BNP ecosystem to 1,938.8 km$^2$.

Geographic information systems (GIS) assessment of habitat allows for more precise evaluation of habitat features and animal use, compared with habitat suitability indices or HEP (Douglas and Leslie 1999). Animal location based models (ALBM) associate GIS data with animal locations to define habitat attributes of used habitats and determine the relationship between used vs. available habitats (Schoenecker 2004). Schoenecker (2004) compared an ALBM to the HEP and determined that 17.6–20.8% of bighorn sheep observations were in areas predicted by the HEP. They concluded that although the HEP had utility, the ALBM was more suitable for the area (Schoenecker 2004). Based on this recommendation, I evaluated the utility of an ALBM with models previously applied to BNP. My objectives were to 1) define escape terrain (i.e., slope) that bighorn sheep locations were most closely associated with and buffer terrain (i.e.,
distance to escape terrain based on a $\geq 50\%$ probability of use) for bighorn sheep in the BNP ecosystem; 2) determine an ALBM based on bighorn sheep locations at BNP; 3) create a model based on DEM data using escape terrain and buffer model (ETBM); and 4) compare the HEP of Sweanor et al. (1995) and Zimmerman et al. (2006) to the ALBM and the ETBM.

**STUDY AREA**

Badlands National Park (Latitude: 43.710880, Longitude: -102.477030) encompasses 98,400 ha and is located in Pennington, Shannon, and Jackson counties within the White River badlands of southwestern South Dakota (Weedon 1999). The badlands of the White River consist of very fine, unconsolidated clay with thin beds of sandstone or isolated concretions (Weedon 1999). Sharp gradients in altitude occur throughout the region with an elevation of 700–1,000 m above mean sea level (Sweanor et al. 1995). Topography of the badlands was formed because of the coincidence of elevation, rainfall, carving action of streams, and the substrate, resulting in slumps, natural bridges, arches, sod tables, toadstools, and isolated flat remnants of the higher plains (Weedon 1999). Vegetated slumps along with mixed-grass prairie sod tables occur in close proximity to the steep badland terrain and are important feeding areas for bighorn sheep (Gamo et al. 1999). Temperature in the BNP ecosystem ranges from -41 to $47^\circ$ C, and annual precipitation averages 41 cm (Weedon 1999). Primary roads in BNP are narrow, asphalt based, and 2-lane. Secondary roads are gravel or unimproved dirt that are maintained by BNP. Roadside shoulders along primary and secondary roads are mowed throughout the summer. Potential mammalian predators of bighorn sheep include
coyotes (*Canis latrans*), and bobcats (*Felis rufus*). Occasional sign or observations of mountain lions (*Puma concolor*) within the area have been reported, their presence and potential impacts on bighorn sheep in this region are unknown but probably limited. Potential herbivore competitors include bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn antelope (*Antilocapra americana*), and black-tailed prairie dogs (*Cynomys ludovicianus*).

The badlands encompass true short-grass prairie, midgrass prairie, and bunch grass types with plant species including western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), blue grama (*Bouteloua gracilis*), needle and thread grass (*Hesperostipa comata*), fringed sage (*Artemisia frigida*), prairie junegrass (*Koeleria macrantha*), little bluestem (*Schizachyrium scoparium*), green sagewort (*A. ludoviciana*), purple coneflower (*Echinacea angustifolia*), and buffalo grass (*Buchloe dactyloides*) (Weedon 1999). Patches of Rocky Mountain juniper (*Juniperus scopulorum*) and eastern red cedar (*J. virginiana*) occur in upper protected draws and slopes (Weedon 1999). Other species, such as plains cottonwood (*Populus delotoides*), peach-leaved willow (*Salix amygdaloides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and American elm (*Ulmus americana*), occur in the deciduous complex along the White River (Weedon 1999). Although 42% of BNP is covered by prairie grasslands, > 46% clay formations on which vegetation is sparse or absent (Von Loh et al. 1999).
METHODS

In September 2004, Badlands National Park (BNP) in conjunction with the South Dakota Department of Game, Fish and Parks and the New Mexico Department of Game and Fish, captured 23 (10 adult females, 2 yearling females, 5 female lambs, and 6 male lambs) Rocky Mountain bighorn sheep from Wheeler Peak in north-central, New Mexico. Bighorn sheep were captured via dropnets and darting (Jessup et. al 1984, Kock et al. 1987). Females were aged based on tooth eruption (Taylor 1962) and wear. Adult and yearling ewes were fitted with colored very high frequency (VHF 150–151 MHz) radio transmitters (250 grams and 1.5 lbs—Advanced Telemetry Systems, Isanti, Minnesota). Lambs were marked with numbered red, yellow, or orange ear tags and were later radio-collared. Captured bighorn sheep were released at Conata Basin Picnic Area near Pinnacles in BNP between 24–27 September. Pinnacles was selected as the release site because it had been identified as a site with suitable habitat (Sweanor et al. 1995) and contained a bighorn sheep subpopulation comprised of 15 individuals (9 males, 3 females, 1 yearling, and 2 lambs) based on a 2003 ground survey. Capture and handling methods followed recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (1998) and were approved by the South Dakota State University Institutional Animal Care and Use Committee.

Radio-collared females were visually relocated ≥ 3 times weekly from September 2004–2006 using handheld and omni directional antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA). Visual daytime locations (Fairaizl 1980), group composition, and behavior (e.g., feeding, bedded, walking) were recorded. All individuals within the
group were identified by radio-collar color, ear tag, or distinguishable markings. Universal transverse Mercator (UTM) position of the individual or group was calculated based on the UTM of the observer collected using a handheld GPS, distance to the animal using a Leica® 1200 rangefinder (Leica Camera AG, Solms, Germany) accurate to ± 1 m, azimuth using a compass, and the vertical angle of the line of sight using a clinometer.

Geographic Information Systems (GIS) analyses were conducted using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA). Data were analyzed using the datum Zone 13N, NAD83. The study area was delineated by merging the 95% adaptive kernel home-ranges for all bighorn sheep located in the Pinnacles area and applying a 1,500-m buffer around the polygon (Chapter 2). I used locational data (n = 585) of resident radio-collared females from the Pinnacles subpopulation collected from May 1992 to November 1994 (Moses et al. 1996, Singer and Gudorf 1999). Escape terrain is the most critical landscape feature for bighorn sheep (Geist 1971, Sweanor et al. 1995) and proximity to escape terrain is an important component in their habitats (Shackelton et al. 1999). Although translocated and resident bighorn sheep differed in their position on slopes, and their proximity to water and roads, they did not statistically differ in their proximity to escape terrain (Chapter 2). Based on the lack of difference in their proximity to escape terrain, a subset of translocated bighorn sheep (n = 585) locations and resident bighorn sheep locations were pooled as the fixed effect for Design II (Manly et al. 2002) and added to the GIS. To compare used and available habitat, random points (n = 1,116) were generated with the HAWTHS TOOLS extension (Beyer 2004) in ArcGIS 9.2. Random points were distributed throughout the
analyses were contingent on the assumption that locations of the bighorn sheep were representative of their use in this area.

Two model sets were created a priori. Model 1 (i.e., ETBM) identified escape terrain and buffer terrain. Model 2 (i.e., ALBM) was created based on a biologically reasonable combination of variables including: vegetation (VEG), distance to roads (D2R), distance to wet areas (D2W), slope (SL), and distance to escape terrain (D2ET) derived from Model 1. I attached the values from raster data to point data for using the intersect point tool (Russell 2006) from the HAWTHS TOOLS extension. Point data from independent (e.g., D2ET, D2W, D2R, SL) and categorical (e.g., VEG) variables were incorporated into the model. Correlation matrices were examined to assess multicollinearity. Model fit was assessed using a Hosmer-Lemeshow test using 10 bins with equal counts per bin (Hosmer and Lemeshow 2000). Logistic regression was used (Manly et al. 2002) to determine the best submodel for predicting habitat selection of bighorn sheep (Schoenecker 2004). Data were analyzed using SYSTAT 11 (Wilkinson 1990).

Escape terrain buffer model

Escape terrain used in the Smith et al. (1991) HEP was defined as slopes > 27° (Sweanor et al. 1995). According the Schoenecker (2004) there was an error in the conversion from percent slope to degree slope in the Smith et al. (1991) HEP; slope used to define escape terrain should have been 30°. To determine the slope bighorn sheep locations were in closer proximity to, I created a slope polygon by delineating all slopes ≥ 22°. Additional polygons were created by increasing the slope value by 5° increments.
(slopes ≥ 27°, slopes ≥ 32°, … slopes ≥ 42°) up to 47°. Each slope polygon was converted to a raster and distance variables were quantified using SPATIAL ANALYST. Distance variables were calculated in kilometers for ease of interpretation. Single variable logistic regression was performed (Manly et al. 2002) in SYSTAT 11 (Wilkinson 1990) to determine the best model to define D2ET. Dichotomous response variables were pooled bighorn sheep locations and random locations. To compare models within a model set, Akaike's Information Criterion for small sample sizes (AICc) was used (Burnham and Anderson 2002). McFadden's rho-squared (MR²) is intended to mimic R² (Steinberg and Colla 1999); therefore, it was used for comparing models within model sets, as well as assessing model performance. According to Hensher and Johnson (1981), MR² values between 0.20 and 0.40 are satisfactory. To determine the reference slope model to use for D2ET, I selected the 2 slope submodels from Model 1 with the highest MR². I adjusted slope values by 1° increments between these 2 submodels until the greatest MR² value was achieved.

To determine the buffer distance to these slopes (i.e., areas proximate to escape terrain), a Resource Selection Probability Function (RSPF) was calculated for the best submodel by transforming the logit (g(x) = β₀ + β₁x₁…βₚ) using equation (Manly et al. 2002):

\[ RSFP = w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 \ldots \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 \ldots \beta_p x_p)} \]
where $\beta_0...\beta_p$ were parameter estimates and $x_1...x_p$ were habitat variable values (van Manen and Pelton 1997, Schoenecher 2004). The ratio of sampling probabilities was not estimated, and thus, RSPF represented an index of selectivity (Manly et al. 2002). The raster calculator in ArcGIS 9.2 was used to map RSFP estimates. Maximum buffer distance to the slope was determined where RSFP was $\geq 0.50$. The best submodel from Model 1 was used in the analysis of Model 2. Because escape terrain and buffer distance were the primary determinants of bighorn sheep habitat (Sweanor et al. 1995), a habitat model for BNP and western South Dakota was created based on the values generated from Model 1.

**Animal location based model**

I converted the vegetation shapefile for BNP (Von Loh et al. 1999) to a raster file, and reclassified the 32 vegetation associations into 6 major vegetation types: grasslands (GR), shrublands (SH), human-use areas (HU), wet areas (WA), woodlands (WO), and unvegetated badlands (BA) (Table 8). Each vegetation type was assigned a value from 0 to 5. The BA category was used as the categorical reference in the model.

Road shape files of Pennington, Jackson, and Shannon counties from the South Dakota Department of Transportation were merged and converted to a raster coverage. Straight-line distances to the road raster and the wet area raster were calculated using SPATIAL ANALYST extension. Distance variables were calculated in km for ease of interpretation. Slope values were determined from a 10-m DEM of the study area with the SPATIAL ANALYST extension. Slope (SLOPE) was calculated in degrees.
Table 8. Area (km\(^2\)) of reclassified vegetation types from Von Loh et al. (1999) at Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Area (km(^2))</th>
<th>Study Area (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>99.232</td>
<td>62.8</td>
</tr>
<tr>
<td>Shrubland</td>
<td>1.782</td>
<td>1.1</td>
</tr>
<tr>
<td>Human-use</td>
<td>0.625</td>
<td>0.4</td>
</tr>
<tr>
<td>Wet Areas</td>
<td>2.177</td>
<td>1.4</td>
</tr>
<tr>
<td>Woodlands</td>
<td>0.986</td>
<td>0.6</td>
</tr>
<tr>
<td>Badlands</td>
<td>53.168</td>
<td>33.7</td>
</tr>
<tr>
<td>Total</td>
<td>157.972</td>
<td>100.000</td>
</tr>
</tbody>
</table>

Logistic regression was used (Manly et al. 2002) to determine the best submodel for predicting habitat selection of bighorn sheep (Schoenecker 2004). Dichotomous response variables were pooled bighorn sheep locations and random locations. Resource Selection Probability Functions (RSPF) were calculated for highly supported models by transforming the logit \( g(x) = \beta_0 + \beta_1 x_1 \ldots \beta_p x_p \) using equation (Manly et al. 2002):

\[
RSFP = w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_1 \ldots \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 \ldots \beta_p x_p)}
\]

where \( \beta_0 \ldots \beta_p \) were the parameter estimates and \( x_1 \ldots x_p \) were the habitat variable values (van Manen and Pelton 1997, Schoenecher 2004). The ratio of sampling probabilities was not estimated and thus, RSPF represented an index of selectivity (Manly et al. 2002). The raster calculator in ArcGIS 9.2 was used to map RSPF estimates. Categories classified by Schoenecher (2004) were used to define habitat suitability: suitable \((0.75 \leq \text{probability of use} \leq 1.0)\), acceptable \((0.50 \leq \text{probability of use} < 0.75)\), marginal \((0.25 \leq \text{probability of use} < 0.50)\), and unsuitable \((0.00 \leq \text{probability of use} < 0.25)\). Areas identified as suitable and acceptable habitats were mapped for BNP.
Validation

To validate the models, I expanded the study area to include the 2 other subpopulations (Cedar Pass, Cedar Butte) of bighorn sheep at BNP. Resident female bighorn sheep locations \((n = 284)\) from the Pinnacles, Cedar Pass, and Cedar Butte subpopulations collected from October 1996 to June 2004 were pooled and added to the GIS; these locations were not used to create the habitat model. The intersect tool from ArcGIS 9.2 was used to determine the number of locations completely contained by the ETBM, the ALBM, and models of Zimmerman et al. (2006) and the Sweanor et al. (1995). Area \((\text{km}^2)\) of suitable bighorn sheep habitat was calculated for each model.

RESULTS

Escape terrain buffer model

Compared with random locations, bighorn sheep locations were closer to slopes \(\geq 40^\circ\) that all other slopes evaluated. Distance to \(40^\circ\) slopes had the greatest \(\text{MR}^2\) \((\text{MR}^2 = 0.379)\) (Fig. 7) and Akaike weight \((w_i = 0.933)\) (Table 9) and was therefore the best model for differentiating bighorn locations from random locations. Slopes \(> 27^\circ\) had been previously used to define escape terrain, but based on my analysis, distance to slopes \(\geq 27^\circ\) performed poorly compared with most other models examined. Slopes \(\geq 40^\circ\) encompassed 1.30 km\(^2\) of the 157.97 km\(^2\) study area (Table 10).
Based on the RSFP, there was a ≥ 50% probability that a bighorn sheep location would be within 285 m of slopes ≥ 40° (Fig. 8). The 285-m buffer value was approximately
Table 10. Area and percent of study area encompassed by slope polygons at Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>Slope (°)</th>
<th>Area (km²)</th>
<th>% of Study Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>≥ 22</td>
<td>11.92</td>
<td>7.55</td>
</tr>
<tr>
<td>≥ 27</td>
<td>7.20</td>
<td>4.56</td>
</tr>
<tr>
<td>≥ 32</td>
<td>4.00</td>
<td>2.53</td>
</tr>
<tr>
<td>≥ 37</td>
<td>2.04</td>
<td>1.29</td>
</tr>
<tr>
<td>≥ 38</td>
<td>1.77</td>
<td>1.12</td>
</tr>
<tr>
<td>≥ 39</td>
<td>1.52</td>
<td>0.96</td>
</tr>
<tr>
<td>≥ 40</td>
<td>1.30</td>
<td>0.83</td>
</tr>
<tr>
<td>≥ 41</td>
<td>1.12</td>
<td>0.71</td>
</tr>
<tr>
<td>≥ 42</td>
<td>0.95</td>
<td>0.60</td>
</tr>
<tr>
<td>≥ 47</td>
<td>0.42</td>
<td>0.27</td>
</tr>
<tr>
<td>Total</td>
<td>157.97</td>
<td>28.57</td>
</tr>
</tbody>
</table>

Figure 8. The Resource selection function probability of the distance of bighorn sheep locations (1992–2006) from slopes ≥ 40° at Badlands National Park, South Dakota, USA.

equal to the 300 m value recommended in the literature (Smith et al. 1991, Sweanor et al. 1995, Schoenecker 2004); therefore, I used a 300-m buffer around slopes ≥ 40° to create the ETBM for BNP and western South Dakota.
Animal location based model

The full model included D2ET, SL, D2R, VEG, and D2W and was the second ranked model with $MR^2 = 0.47$ and $AIC_w = 0.40$ (Table 11). The final model, which included D2ET, D2R, VEG, and D2W, had an $MR^2 = 0.47$ but $AIC_w = 0.61$. The final model had reasonable fit (Hosmer-Lemeshow $P = 0.322$, df = 7). Based on the odd’s ratio of the final model, bighorn sheep were $\approx 1,000 \times$ less likely to inhabit an area 1 km from $40^\circ$ slopes than a location adjacent to $40^\circ$ slopes, $\approx 1.6 \times$ less likely to inhabit an area 1 km from a road than a location adjacent to a road, and $\approx 5 \times$ less likely to inhabit an area 1 km from a wet area than a location adjacent to a wet area (Table 12). Bighorn sheep were $\approx 144 \times$ more likely to inhabit human-use areas than badlands and were $\approx 7 \times$ more likely to inhabit woodlands than badlands. Grasslands, shrublands, and water areas were used in equal proportion to the categorical reference badlands.

Validation

Of the bighorn sheep locations that were not used to create the model, 95.4% and 88.7% of the locations were completely contained by the ALBM and ETBM, respectively whereas, the Sweanor et al. (1995) and the Zimmerman et al. (2006) model contained 87.7% and 91.2%, respectively, of the points (Table 13). Of the 981 km$^2$ study area in BNP, $\approx 464$ km$^2$ and 367 km$^2$ of suitable bighorn sheep habitat was identified by the ALBM and ETBM, respectively (Table 13). A total of 335.0 km$^2$ was overlapped by both models (Fig. 9). The Sweanor et al. (1995) and Zimmerman et al. (2006) models identified $\approx 377$ km$^2$ and 599 km$^2$, respectively, of suitable bighorn sheep habitat in BNP (Table 13).
Table 11. Habitat selection models created from bighorn sheep locations collected in 1992–2006 in Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>#</th>
<th>(w_i)</th>
<th>Model</th>
<th>(^2\text{AICc})</th>
<th>(\Delta\text{AIC}_c)</th>
<th>(K)</th>
<th>(^4\text{MR}^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.61</td>
<td>3.304 - 7.442 (D2ET) - 0.498 (D2R) - 1.613 (D2W) + 0.019 (GR) - 0.499 (SH) + 4.974 (HU) + 0.885 (WA) + 1.948 (WO)</td>
<td>1698.88</td>
<td>0</td>
<td>10</td>
<td>0.47</td>
</tr>
<tr>
<td>2</td>
<td>0.39</td>
<td>3.432 - 7.598 (D2ET) - 0.007 (SL) - 0.505 (D2R) - 0.037 (GR) - 0.551 (SH) + 4.998 (HU) + 0.869 (WA) + 1.935 (WO) - 1.586 (D2W)</td>
<td>1699.76</td>
<td>0.88</td>
<td>11</td>
<td>0.47</td>
</tr>
<tr>
<td>3</td>
<td>0.00</td>
<td>3.419 - 6.941 (D2ET) - 0.527 (D2R) - 1.694 (D2W)</td>
<td>1765.48</td>
<td>66.59</td>
<td>5</td>
<td>0.45</td>
</tr>
<tr>
<td>4</td>
<td>0.00</td>
<td>3.482 - 7.065 (D2ET) - 0.528 (D2R) - 0.005 (SL) - 1.666 (D2W)</td>
<td>1766.90</td>
<td>68.01</td>
<td>6</td>
<td>0.45</td>
</tr>
<tr>
<td>5</td>
<td>0.00</td>
<td>2.820 - 8.210 (D2ET) - 1.751 (D2W) + 0.280 (GR) - 0.056 (SH) + 6.074 (HU) + 1.155 (WA) + 1.857 (WO)</td>
<td>1768.81</td>
<td>69.93</td>
<td>9</td>
<td>0.45</td>
</tr>
<tr>
<td>6</td>
<td>0.00</td>
<td>2.635 - 6.247 (D2ET) - 0.590 (D2R) - 0.014 (SL)</td>
<td>1846.64</td>
<td>147.75</td>
<td>5</td>
<td>0.42</td>
</tr>
<tr>
<td>7</td>
<td>0.00</td>
<td>2.390 - 0.592 (D2R) - 5.822 (D2ET)</td>
<td>1850.81</td>
<td>151.92</td>
<td>4</td>
<td>0.42</td>
</tr>
<tr>
<td>8</td>
<td>0.00</td>
<td>1.612 + 0.492 (GR) + 0.485 (SH) + 6.141 (HU) + 1.813 (WA) + 2.092 (WO) - 7.225 (D2ET)</td>
<td>1861.54</td>
<td>162.65</td>
<td>8</td>
<td>0.42</td>
</tr>
<tr>
<td>9</td>
<td>0.00</td>
<td>2.041 - 0.016 (SL) - 6.656 (D2ET)</td>
<td>1966.90</td>
<td>268.02</td>
<td>4</td>
<td>0.38</td>
</tr>
<tr>
<td>10</td>
<td>0.00</td>
<td>1.770 - 6.168 (D2ET)</td>
<td>1972.73</td>
<td>273.85</td>
<td>3</td>
<td>0.38</td>
</tr>
<tr>
<td>11</td>
<td>0.00</td>
<td>0.581 - 1.242 (GR) - 0.340 (SH) + 3.578 (HU) - 2.191 (WA) + 1.677 (WO)</td>
<td>2843.15</td>
<td>1144.27</td>
<td>7</td>
<td>0.11</td>
</tr>
<tr>
<td>12</td>
<td>0.00</td>
<td>-0.647 + 0.075 (SL)</td>
<td>2899.93</td>
<td>1201.05</td>
<td>3</td>
<td>0.09</td>
</tr>
</tbody>
</table>

\(^1\)wi = Akaike weights, \(^2\)AICc = Akaike's Information Criterion for small sample sizes, \(^3\)K = number of parameters, \(^4\)MR² = McFadden's rho-squared, D2ET = Distance to slopes > 40, D2R = Distance to road, D2W = Distance to wet areas, GR = Grasslands, SH = Shrublands, HU = Human-use areas, WA= Wet areas, WO = Woodlands, SL = Slope.
Table 12. Estimated odds ratios for variables in the final bighorn sheep habitat selection model created from bighorn sheep locations collected in 1992–2006 in Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Odds Ratio</th>
<th>95% CI Upper</th>
<th>Lower</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>D2ET</td>
<td>0.001</td>
<td>0.001</td>
<td>0.000</td>
<td>≈ 1000 × less likely to inhabit an area 1 km from 40° slopes than a location adjacent to 40° slopes</td>
</tr>
<tr>
<td>D2RS</td>
<td>0.608</td>
<td>0.684</td>
<td>0.541</td>
<td>≈ 1.6 × less likely to inhabit an area 1 km from a road than a location adjacent to a road</td>
</tr>
<tr>
<td>D2W</td>
<td>0.199</td>
<td>0.289</td>
<td>0.137</td>
<td>≈ 5 × less likely to inhabit an area 1 km from a wet area than a location adjacent to a wet area</td>
</tr>
<tr>
<td>GR</td>
<td>1.019</td>
<td>1.352</td>
<td>0.767</td>
<td>As likely to inhabit grasslands as badlands</td>
</tr>
<tr>
<td>SH</td>
<td>0.607</td>
<td>2.201</td>
<td>0.168</td>
<td>As likely to inhabit shrublands as badlands</td>
</tr>
<tr>
<td>HU</td>
<td>144.656</td>
<td>1290.988</td>
<td>16.209</td>
<td>≈ 144 × more likely to inhabit human-use areas than badlands</td>
</tr>
<tr>
<td>WA</td>
<td>2.424</td>
<td>10.969</td>
<td>0.536</td>
<td>As likely to inhabit wet areas as badlands</td>
</tr>
<tr>
<td>WO</td>
<td>7.013</td>
<td>16.851</td>
<td>2.918</td>
<td>≈ 7 × more likely to inhabit woodlands than badlands</td>
</tr>
</tbody>
</table>

D2ET = Distance to slopes > 40, D2R = Distance to road, D2W = Distance to wet areas, GR = Grasslands, SH = Shrublands, HU = Human-use areas, WA = Wet areas, WO = Woodlands.

Table 13. Comparison of suitable bighorn sheep habitat models created from bighorn sheep locations collected in 1992–2006 in Badlands National Park, South Dakota, USA.

<table>
<thead>
<tr>
<th>Model</th>
<th># Locations</th>
<th>Locations (%)</th>
<th>Area (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Escape terrain and buffer model</td>
<td>252</td>
<td>88.7</td>
<td>366.59</td>
</tr>
<tr>
<td>Animal location based model</td>
<td>259</td>
<td>95.4</td>
<td>463.96</td>
</tr>
<tr>
<td>Sweanor et al. (1995) model</td>
<td>249</td>
<td>87.7</td>
<td>376.86</td>
</tr>
<tr>
<td>Zimmerman et al. (2006) model</td>
<td>271</td>
<td>91.2</td>
<td>598.62</td>
</tr>
<tr>
<td>Total</td>
<td>284</td>
<td>100.0</td>
<td>981.72</td>
</tr>
</tbody>
</table>
Figure 9. Suitable bighorn sheep habitat identified by the Escape Terrain and Buffer Model and the Animal Location Based Model created from bighorn sheep locations collected in 1992–2006 at Badlands National Park, South Dakota, USA.

Based on the ETBM, 4,007.2 km$^2$ of 108,362 km$^2$ was identified as suitable bighorn sheep habitat in western South Dakota (Fig. 10). The largest patches of suitable habitat were located in the Black Hills, the BNP ecosystem, portions of the Pine Ridge Indian Reservation, and areas adjacent to the Moreau and Grand rivers in north-central South Dakota. Small habitat patches also were identified in Harding County in northwestern South Dakota.
Figure 10. Suitable bighorn sheep habitat based on the Escape Terrain and Buffer Model created from bighorn sheep locations collected from 1992 to 2006 in western South Dakota, USA.

**DISCUSSION**

Escape terrain and proximity to escape terrain were the most critical habitat features for bighorn sheep, defining distribution of the species throughout its range (Geist 1971, Van Dyke 1983, Shackleton et al. 1999, Swenanor et al. 1995). Escape terrain is often qualitatively defined as steep, rough, rugged, rocky, and/or precipitous terrain but quantitative descriptions are either lacking (Shannon et al. 1975, Van Dyke 1983), or variable between habitats and populations (Shackleton et al. 1999). Escape terrain values
used in habitat selection studies or habitat models have ranged from > 27° (Smith et al. 1991) to ≥ 36° (Turner et al. 2004). Sweanor et al. (1995) numerically defined escape terrain utilized by bighorn sheep at BNP as slopes > 27°. This quantitative description of escape terrain was based on the recommendations of Smith et al. (1991) for montane populations. Based on my analysis, locations of bighorn sheep in BNP were more often proximately located near slopes ≥ 40° compared with all other slopes examined (e.g., 22°, 27°, 32° …47°). Fairbanks et al. (1987) also reported a greater use of steeper slopes (e.g., 31.4–38.7°) for a prairie population of bighorn sheep in northwestern Nebraska. The selection for steeper slopes in prairie populations may be a function of more topographic variability and erodible soil types (e.g., clay) in prairie compared with montane habitats.

Distribution of escape terrain determines the extent to which other habitat features are used (Van Dyke 1983). In general, as the distance from escape terrain increases, the use of the habitat decreases, but the distance from escape terrain may fluctuate in response to disturbance from humans or predators (Van Dyke 1983). According to my ALBM, female bighorn sheep at BNP were usually located within 285 m of 40° slopes. These results support those of Fairbanks et al. (1985) and others that bighorn sheep prefer areas < 300 m from escape terrain (Smith et al. 1991, Sweanor et al. 1995, and Schoenecker 2004). Turner et al. (2004) determined that escape terrain was a low priority for Nelson’s bighorn sheep. They speculated that this finding may have been due to the habituation of bighorn sheep to human-use areas where predation pressures were reduced. In my study, resident bighorn sheep were closer to escape terrain and farther
from human-use areas than introduced bighorn sheep (Chapter 3). As previously mentioned, translocated bighorn sheep were highly acclimated to the presence of humans in their former range. This may have been due in part to feeding of the bighorn sheep by visitors to the Taos Ski Valley. The acclimation of the translocated bighorn sheep at BNP to the presence of humans may have increased the average distance of locations to escape terrain, inflating the overall value of the distance of bighorn sheep to escape terrain (Papouchis et al. 2001). Furthermore, the acclimation of bighorn sheep to humans may have influenced the selection of human-use areas in the model. Human-use areas comprised < 0.5 % of the study area at BNP, but those areas occurred in close proximity to escape terrain where abundant sources of native and non-native forage exist. Therefore, selection for human-use areas may have been a function of the proximity of these areas to escape terrain and foraging areas, rather than a predator avoidance tactic or acquisition of processed human foods.

Like human-use areas, woodlands comprised a small portion of the study area (< 0.7%). According to Smith et al. (1991), bighorn sheep typically avoid dense conifer stands where visibility is < 55% due to their dependency on vision to detect predators (Van Dyke 1983). Yet, bighorn sheep at BNP selected woodland habitats. Other studies demonstrated that bighorn sheep selected conifer stands for thermoregulation (Fairbanks et al. 1987, Schoenecher 2004). The thermal neutral zone of bighorn sheep is -20–20° C (Chappel and Hudson 1978). If temperature decreases from -20° C to -30° C, there is a 37–39% increase in the metabolic rate of bighorn sheep, and if winds exceed 8 m/sec when temperatures are < -20° C, additional increases in metabolic costs can occur.
(Chappel and Hudson 1978). Previous seasonal habitat analysis at BNP, demonstrated that female bighorn sheep were located in juniper cover types during rut and winter (Singer and Gudorf 1999), providing support for a thermoregulatory advantage. Van Dyke (1983) also documented that bighorn sheep used woodland habitats for shade during hot summer months. Seasonal evaluation of habitat selection may provide more insight to resource requirements of bighorn sheep at BNP.

As documented in other ecosystems (Smith et al. 1991, Schoenecher 2004, Turner et al. 2004), water sources were an important variable for determining suitable bighorn sheep habitat in BNP. The distance (< 1 km) of bighorn sheep locations from areas identified as wet (Chapter 3) were similar to those reported in other studies (Smith et al. 1991, Schoenecher 2004, Turner et al. 2004). Bighorn sheep use numerous sources to acquire free water including dew, snow, streams, ponds, springs, and lakes (Van Dyke 1983). Water also can be acquired through the consumption of succulent vegetation (Van Dyke 1983, Turner et al. 2004). Because of the numerous sources of water, evaluating water availability in this study was challenging. Based on the vegetation layer, ≈ 2 km² of wet areas were identified in the study area, but springs and seeps, which occur throughout the ecosystem, were not identified in the GIS because of size. Furthermore, because of the clay soil type in BNP, water is retained in shaded arroyos following weather events. Although the extent of these pools throughout the study area, the duration of retention of water in these pools, and the use of these pools by wildlife has not been evaluated, observations of tracks around these areas indicated use by bighorn sheep. Until all sources of water are evaluated, it is difficult to determine if water is a
limiting factor for bighorn sheep at BNP. Future analysis should focus on evaluation of availability and use of multiple sources of water to determine their effects on the distribution and abundance of bighorn sheep at BNP.

Models by Sweanor et al. (1995) and Zimmerman et al. (2006) differed in size of pixel used in the analyses (30-m vs. 10-m, respectively). The model by Zimmerman et al. (2006) identified more suitable bighorn sheep habitat than the model by Sweanor et al. (1995) but that was due to more slopes > 27° being identified by the 10-m DEM data than the 30-m DEM data. When the model by Zimmerman et al. (2006) was validated, it performed better (91.2% of locations) than the model by Sweanor et al. (1995) (87.7% locations). That result was probably reflected by more habitat being identified by the model of Zimmerman et al. (2006) than the model of Sweanor et al. (1995). The model by Zimmerman et al. (2006) and the ETBM of this study differed only on the basis of how escape terrain was defined. Zimmerman et al. (2006) used > 27° slopes and the ETBM used slopes ≥ 40°. More bighorn sheep habitat was identified and more locations were contained within the model by Zimmerman et al. (2006) than the ETBM, but the difference was due to the greater availability of slopes > 27° (7.2 km²) than slopes ≥ 40° (1.3 km²) in the BNP study area. More suitable bighorn sheep habitat was identified by the ALBM (464 km²) than the ETBM (367 km²), but a total of 335.0 km² overlapped in both models. The overlap was a result of the importance of the independent variable D2ET. The ALBM performed the best (95.4% of locations) at predicting bighorn sheep locations compared with all other models evaluated, but it required specific GIS data for analysis (e.g., vegetation data), which is not currently available across all landscapes.
Until these data are available, the ETBM may serve as a suitable predictor of bighorn sheep habitat.

Based on the ETBM, 4,007.2 km\(^2\) of 108,362 km\(^2\) was identified as suitable bighorn sheep in western South Dakota. The largest patches of suitable habitat were located in the Black Hills and the BNP ecosystem. The ETBM model was created from data from a prairie population of bighorn sheep; therefore, its applicability to areas in the Black Hills may be limited. The model should be validated with locations of bighorn sheep in the Black Hills ecosystem before it widely applied for management. Areas of suitable habitat also were identified adjacent to the Moreau and Grand rivers and in the Slim Buttes in northwestern South Dakota. Limited reports exist describing the distribution of bighorn sheep in South Dakota outside of the Black Hills and the badlands (Buechner 1960). Because most of the large predators (e.g., wolves \([\text{Canis lupus}]\)) of bighorn sheep have been extirpated from the state, some of these areas may now be suitable for the species. The limiting factors in areas outside of the Black Hills and badlands will be the availability of critical lambing habitat and the extent of the distribution of domestic sheep.

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CHAPTER 4

POPULATION HISTORY AND GENETIC STRUCTURE OF BIGHORN SHEEP
AT BADLANDS NATIONAL PARK: PRE- AND POST-AUGMENTATION
INTRODUCTION

The Audubon’s bighorn ecotype (Ovis canadensis auduboni [Merriam 1901] now O. c. canadensis [Shaw 1804]), described as a subspecies of bighorn sheep (Cowan 1940), inhabited the badlands of the Yellowstone and Missouri rivers in eastern Montana, eastern Wyoming, western North and South Dakota, and northwestern Nebraska (Valdez and Krausman 1999) with the eastern extent of its range occurring in the South Dakota badlands (Buechener 1960). According to documentation from Maximilian the Prince of Weid in 1834, the bighorns, “abounded in the Mauvaises Terres” (a.k.a. the South Dakota badlands) (Thwaites 1906). The introduction of domestic sheep to the Badlands National Park (BNP) ecosystem in 1894 (Hall 1997) coupled with unrestricted subsistence and trophy hunting likely led to the extirpation of bighorn sheep from the area (Buechner 1960). The last known Audubon’s bighorn in South Dakota was harvested in 1924 or 1925 in Washabaugh (a.k.a. south Jackson) County, near the present day location of Badlands National Park (BNP).

The South Dakota Department of Game, Fish and Parks (SDGFP) initiated a Memorandum of Understanding (MOU) with the National Park Service (NPS) to reestablish a population of bighorn sheep at BNP in the 1960’s. The goal of the agreement between the NPS and SDGFP was to establish a captive herd that would serve as a source for translocations into other areas of South Dakota, initiating additional populations within BNP as well as 2 locations in the northwestern part of the state (Hjort and Hodgins 1964). National Park Service Management Policy states that the agency will maintain as part of the natural ecosystems of parks all native flora and fauna and will
strive to restore extirpated native plant and animal species to parks if the population can be self-perpetuating (National Park Service 2006). In 1964, the NPS cooperated with the SDGFP and the Colorado Division of Wildlife to translocate 22 Rocky Mountain bighorn sheep (Ovis canadensis canadensis) from Pikes Peak, Colorado, to BNP (Bessken and Plumb 1997). The animals were placed in a 150-hectare enclosure located approximately 1 km west of the Conata Road Picnic Area (i.e., Pinnacles) (Fig. 11).

For nearly 3 years the BNP bighorn sheep population was stable, but during late-summer 1967, a loss of ≈ 50% occurred to the enclosed population, which was attributed to Pasteurella infection (Hazeltine 1967, Powell 1967, Weide 1967), and reduced the population to 14 individuals (2 females, 2 males, 4 yearling females, and 6 lambs). The surviving animals were released on 31 August 1967 (Badlands National Park Bighorn Sheep Restoration Program 1969). For 2 years, periodic, opportunistic observations suggested that a herd of 10–12 animals remained within 2 km of the release site (Badlands National Park Bighorn Sheep Restoration Program 1969).

The first post-release population survey was conducted in June 1980. During a 1-man, 1-week ground survey, 27 bighorn sheep (9 females, 8 males, 2 yearlings, and 8 lambs) were observed within a 13.5-km² area adjacent to the release enclosure (McCutchen 1980). McCutchen (1980) considered the population to be stable but not
increasing based on a lamb:ewe ratio of 22:100 derived from his survey. No definitive factors limiting population growth were identified although water, forage, and genetic factors were considered (McCutchen 1980).

During the early 1980’s, the population continued to inhabit a 40-km² area in the Pinnacles region of BNP. From 1987–1990, SDGFP, under the MOU, conducted winter ground counts in the North Unit of BNP. Based on observations of 93 animals, SDGFP estimated a population of 133–200 bighorn sheep with a lamb:ewe ratio of 53:100 during the winter of 1989–90 (Benzon 1992). During an aerial survey in September 1991, 30
bighorn sheep were observed in the South Unit of Badlands National Park, approximately 20 km south of the Pinnacles population. Qualitative accounts from local ranchers suggest that a small band had been established in the South Unit of the Park as early as 1981 (Badlands National Park Resource Management Plan and Environmental Assessment 1984). During 1992–1994, BNP captured and radio-collared male and female bighorn sheep. Using the sightability model developed by Unsworth et al. (1994), estimated population size was 163 ± 55 (90% CI) individuals in the North and South Units. Aerial surveys in October 1994 indicated a lamb:ewe ratio of 39:100.

Sweanor et al. (1995) evaluated bighorn sheep habitat in the greater BNP area as an aid to restoration of bighorn sheep throughout their historical ranges. Using the habitat parameters and model for evaluating bighorn sheep habitat developed by Smith et al. (1991) and refined by Sweanor et al. (1995), it was estimated that BNP could sustain 400–600 bighorn sheep. Sweanor et al. (1995) reported that a total of 802 km² of 5,322 km² was suitable bighorn sheep habitat at BNP. They also determined that 3,012 km², 1,410 km², and 503 km² (summer, winter, and lambing range, respectively), was suitable bighorn sheep habitat (Sweanor et al. 1995).

In 1996, 12 females and 4 males from the Pinnacles area in the North Unit were captured, radio-collared, and translocated to Cedar Pass (Fig. 11). A period of heavy population decline and poor recruitment from 1995 to 1997 was attributed to an outbreak of epizootic hemorrhagic disease or bluetongue. A November 2000 survey documented that the BNP population contained a minimum of 58 individuals occupying 3 separate habitat patches. However, 1 case of bluetongue was documented from the carcass of a
radio-collared female in the Cedar Pass Area in October 2000, and 3 other collared females were found dead in the South Unit during the November 2000 survey. Cause of death for these 3 females, all ≥ 6 years of age, was unknown. A pronghorn antelope (*Antilocapra americana*) found dead in the North Unit of the BNP in September also was documented with bluetongue. By 2001, bighorn sheep in the North Unit of BNP had reached a low of 37 individuals.

Although the original founder population of bighorn sheep at BNP was 14 animals, the estimated effective population size for the BNP population was 6, counting only adults and yearlings. Assuming all of these individuals survived and reproduced, the maximum effective population size was ≈ 12.9 (Singer 2000). Recommendations to restore the genetic diversity of bighorn sheep included a mixed-sex augmentation (*n* > 30) of bighorn sheep from an outbred native source population of Rocky Mountain bighorn sheep (Ramey et al. 2000). A mixed-sex augmentation was recommended because it would provide short-term and long-term genetic contributions to the BNP population (Ramey et al. 2000). Ramey et al. (2000) further recommended that the introduced bighorn sheep should serve to both augment the current population and establish a new subpopulation to add to the existing 3 subpopulations in BNP.

Shackleton and the International Union for Conservation of Nature and Natural Resources (IUCN)/Species Survival Commission (SCC) Caprinae Specialist Group (1997) also had determined that the ecotypes of bighorn sheep in the mixed-grass badlands were not secure because there were few reserves and protected areas and few of these areas contained bighorn sheep. Thus, conservation measures proposed by the
IUCN/SCC were to expand populations and distribution of bighorn sheep throughout its range in the eastern mixed-grass prairie (Shackleton and the IUCN/SCC Caprinae Specialist Group 1997).

In September 2004, BNP in conjunction with the SDGFP and the New Mexico Department of Game and Fish, translocated 23 Rocky Mountain bighorn sheep from Wheeler Peak, New Mexico to BNP. The objectives of this study were to 1) determine degree of population subdivision ($F_{st}$) between the North and South Units of BNP and 2) evaluate the observed heterozygosity ($H_o$), expected heterozygosity ($H_e$), number of alleles per locus, average number of alleles per locus ($N_e$), and the number of effective alleles ($N_{ea}$) of bighorn sheep at BNP, pre- and post-augmentation. I hypothesized that 1) due of historic movements of radio-collared male bighorn sheep between the north and south units (E. Childers, National Park Service, personal communication), $F_{st}$ would be close to 0 indicating interbreeding between the 2 Units and 2) genetic parameters evaluated would increase following augmentation due to genetic variation in the outbred source of translocated bighorn sheep (Hogg et al. 2006).

**STUDY AREA**

Badlands National Park (Latitude: 43.710880, Longitude: -102.477030) encompasses 98,400-ha and is located in Pennington, Shannon, and Jackson counties within the White River badlands of southwestern South Dakota (Weedon 1999). The badlands of the White River consist of very fine, unconsolidated clay with thin beds of sandstone or isolated concretions (Weedon 1999). Sharp gradients in altitude occur throughout the region with elevation ranging from 700 to 1,000 m above mean sea level.
Topography of the badlands was formed because of the coincidence of elevation, rainfall, carving action of streams, and the substrate, resulting in slumps, natural bridges, arches, sod tables, toadstools, and isolated flat remnants of the higher plains (Weedon 1999). These vegetated slumps along with mixed-grass prairie sod tables occur in close proximity to the steep badland terrain and are important feeding areas for bighorn sheep (Gamo et al. 1999). Temperature in the BNP ecosystem ranges from -41 to 47° C, and annual precipitation averages 41 cm (Weedon 1999). Primary roads in BNP are narrow, asphalt based, and 2-lane. Secondary roads are gravel or unimproved dirt that are maintained by BNP. Roadside shoulders along primary and secondary roads are mowed throughout the summer. Potential mammalian predators of bighorn sheep include coyotes (Canis latrans), and bobcats (Felis rufus). Occasional sign or observations of mountain lions (Puma concolor) within the area have been reported, their presence and potential impacts on bighorn sheep in this region are unknown but probably limited. Potential herbivore competitors include bison (Bison bison), mule deer (Odocoileus hemionus), white-tailed deer (O. virginianus), pronghorn antelope (Antilocapra americana), and black-tailed prairie dogs (Cynomys ludovicianus).

The badlands encompass true short-grass prairie, midgrass prairie, and bunch grass types with plant species including western wheatgrass (Pascopyrum smithii), green needlegrass (Nassella viridula), blue grama (Bouteloua gracilis), and needle and thread grass (Hesperostipa comata), fringed sage (Artemisia frigida), prairie junegrass (Koeleria macrantha), little bluestem (Schizachyrium scoparium), green sagewort (A. ludoviciana), purple coneflower (Echinacea angustifolia), and buffalo grass (Buchloe dactyloides).
(Weedon 1999). Patches of Rocky Mountain juniper (*Juniperus scopulorum*) and eastern red cedar (*J. virginiana*) occur in upper protected draws and slopes (Weedon 1999). Other species, such as plains cottonwood (*Populus delotoiides*), peach-leaved willow (*Salix amygdaloides*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and American elm (*Ulmus americana*), occur in the deciduous complex along the White River (Weedon 1999). Although 42% of BNP is covered by prairie grasslands, over 46% is clay formations on which vegetation is sparse or absent (Von Loh et al. 1999).

**METHODS**

In September 2004, 23 (10 adult females, 2 yearling females, 5 female lambs, and 6 male lambs) Rocky Mountain bighorn sheep were translocated to BNP from Wheeler Peak, New Mexico. Bighorn sheep were captured via dropnets and darting (Jessup et. al 1984, Kock et al. 1987). Females were aged based on tooth eruption (Taylor 1962) and wear. Adult and yearling ewes were fitted with colored very high frequency (VHF150–151 MHz) radio transmitters (250 grams and 1.5 lbs—Advanced Telemetry Systems, Isanti, Minnesota). Lambs were marked with numbered red, yellow, or orange ear tags and were later fitted with VHF radio-collars. Captured bighorn sheep were released at Conata Basin Picnic Area near Pinnacles in BNP between 24–27 September. Pinnacles was selected as the release site because it had been identified as a site with suitable habitat (Sweanor et al. 1995) and contained a subpopulation comprised of 15 individuals (9 males, 3 females, 1 yearling, and 2 lambs) based on a 2003 ground survey (Eddie Childers, National Park Service, personal communication). From November 2005–2006, 5 (2 male, 3 females) first generation offspring (F1) were captured using a net-gun and
eartagged. Three female F1 were captured and radio-collared from November 2006–May 2007. Blood samples were collected from all captured animals via jugular or cephalic venipuncture for DNA extraction. Tissue samples were collected from 4 additional F1 that were euthanized due to contact with domestic sheep (see Chapter 2). Capture and handling methods followed recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (1998) and were approved by the South Dakota State University Institutional Animal Care and Use Committee.

Samples were collected from individuals alive during 7 time periods (e.g., Bighorn sheep which occurred in the BNP ecosystem prior to 1925 [Historic], 1992, 1996, 1998, adult males born prior to the augmentation [Adult04], augmented bighorn sheep [NMIntro], offspring of the augmentation [Off0506]). Blood samples had been collected from resident bighorn sheep captured in the north and south units of BNP in 1992, 1994, 1998, and 2004–2005 (Adult04). Turbinate bone or tissue samples were collected from skulls of bighorn sheep of known origin collected by BNP employees from 1992–2007. Turbinate bone samples also were collected from Historic samples. Genomic DNA from blood and tissue samples was extracted following the standard DNA extraction methods in the DNeasy Tissue Kit (Qiagen Inc., Valencia, California, USA). DNA from historic bone samples was extracted following recommended protocols for ancient DNA (Herrmann and Hummel 1994, Hofreiter et al. 2001, Wisely et al. 2004, Gilbert et al. 2005). DNA was amplified with polymerase chain reaction (PCR) and standard microsatellite typing procedures for 8 widely used ‘neutral’ microsatellite DNA
markers (Forbes and Hogg 1999) and for 7 loci in genes of known function (Luikart et al. 2008) (Table 14).

The reaction volumes (10 μl) contained 1.0-3.0μL DNA, 1 × reaction buffer (Applied Biosystems, Foster City, California, USA), 2.0 mM MgCl₂, 200μM of each dNTP, 1μM reverse primer, 1μM dye-labeled forward primer, 1.5 mg/ml BSA, and 1U Taq polymerase (Applied Biosystems, Foster City, California, USA). The PCR profile was 94°C/5 min, (94°C/1 min, 54-58°C/1 min, 72°C/30s) × 29 cycles for tissue and blood samples, and was increased to 45 cycles for use with historical samples. PCR products were run in a 6.5% acrylamide gel for 2 hours on a LI-COR DNA analyzer (LI-COR Biosciences, Lincoln, Nebraska, USA). GENEPOP 4.0 (Raymond and Rousset 1995) was used to determine \( F_{st} \), \( H_o \), \( H_e \), \( N_e \), and \( N_{ea} \). Alpha was set at 0.05.

**RESULTS**

DNA was extracted and successfully genotyped from a total of 95 individuals (Historic: \( n = 3 \), 1992: \( n = 26 \), 1996: \( n = 14 \), 1998: \( n = 14 \), Adult04: \( n = 3 \), NMIntro: \( n = 23 \), Off0506: \( n = 12 \)). Fifteen (8 neutral loci, 7 in genes of known function) polymorphic loci were genotyped across the 7 time periods (Table 14). Seven loci from 4 populations deviated from Hardy-Weinberg equilibrium (Table 15). When all loci were examined, number of alleles per locus was 3–9 with the lowest variation in the KRT2 and KERA loci and the greatest variation in SOMAb and HH6s loci (Table 14).

<table>
<thead>
<tr>
<th>Locus name</th>
<th># alleles</th>
<th>Base pairs</th>
<th>Function</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Neutral loci</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAF36</td>
<td>8</td>
<td>87–105</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>MAF48</td>
<td>6</td>
<td>116–126</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>FCB304</td>
<td>5</td>
<td>131–139</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>AE16</td>
<td>8</td>
<td>74–96</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>HH62</td>
<td>9</td>
<td>111–127</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>MAF209</td>
<td>7</td>
<td>105–119</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>MAF33</td>
<td>4</td>
<td>122–128</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td>FCB266</td>
<td>6</td>
<td>80–92</td>
<td></td>
<td>Forbes and Hogg 1999</td>
</tr>
<tr>
<td><strong>Loci in genes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KRT2</td>
<td>3</td>
<td>125–133</td>
<td>Keratin production</td>
<td>McLaren et al. 1997</td>
</tr>
<tr>
<td>KERA</td>
<td>3</td>
<td>173–177</td>
<td>Keratin production</td>
<td>J. F. Maddox, unpublished</td>
</tr>
<tr>
<td>SOMA</td>
<td>9</td>
<td>92–126</td>
<td>Growth hormone receptor</td>
<td>Lucy et al. 1998</td>
</tr>
<tr>
<td><strong>Loci in candidate genes</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADCYAP1</td>
<td>5</td>
<td>79–103</td>
<td>Activates production of T-helper cell 2</td>
<td>Wood and Phua 1994</td>
</tr>
<tr>
<td>TCRG4</td>
<td>5</td>
<td>166–178</td>
<td>T-cell receptor gene</td>
<td>Diez-Tascón et al. 2002</td>
</tr>
<tr>
<td>MMP9</td>
<td>5</td>
<td>181–193</td>
<td>Codes for enzyme involved in lung tissue repair</td>
<td>Maddox 2001</td>
</tr>
<tr>
<td>OLADRBps</td>
<td>7</td>
<td>267–291</td>
<td>Major histocompatibility class II gene</td>
<td>Blattman and Beh 1992</td>
</tr>
</tbody>
</table>

\( F_s \) is a metric of subdivision and measures differences in gene frequency (Allendorf and Luikart 2007). Values close to 0.00 indicate that interbreeding is occurring between populations, whereas values close to 1.00 indicate complete substructure (Allendorf and Luikart 2007). Based on the evaluation of 7 neutral loci of
resident bighorn sheep from the north unit \( n = 52 \) and south unit \( n = 14 \) of BNP, \( F_{st} = 0.013 \)


<table>
<thead>
<tr>
<th>Population</th>
<th>Locus</th>
<th>P-value</th>
<th>S.E</th>
<th>W&amp;C</th>
<th>R&amp;H</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>MAF36</td>
<td>0.0370</td>
<td>0.0030</td>
<td>0.411</td>
<td>0.332</td>
</tr>
<tr>
<td></td>
<td>MAF48</td>
<td>0.0351</td>
<td>0.0040</td>
<td>0.121</td>
<td>0.311</td>
</tr>
<tr>
<td></td>
<td>HH62</td>
<td>0.0014</td>
<td>0.0007</td>
<td>0.174</td>
<td>0.022</td>
</tr>
<tr>
<td></td>
<td>ADCYAP1</td>
<td>0.0020</td>
<td>0.0003</td>
<td>-0.385</td>
<td>-0.204</td>
</tr>
<tr>
<td>1996</td>
<td>TCRG4</td>
<td>0.0163</td>
<td>0.0017</td>
<td>0.437</td>
<td>0.529</td>
</tr>
<tr>
<td>1998</td>
<td>KERA</td>
<td>0.0325</td>
<td>0.0010</td>
<td>0.766</td>
<td>0.827</td>
</tr>
<tr>
<td>NMIntro</td>
<td>MAF36</td>
<td>0.0287</td>
<td>0.0031</td>
<td>0.143</td>
<td>0.097</td>
</tr>
</tbody>
</table>

SE = standard error, W & C = Weir and Cockerham’s (1984) \( F_{is} \) estimate, R&H = Robertson and Hill’s (1984) \( F_{is} \) estimate.

(95% CI = 0.0-0.3) with \( \approx 11.7 \) migrants occurring per generation. I used a G-test to evaluate population differentiation based on all loci; gene frequency did not differ \( (\chi^2 = 14.411, df = 14, P = 0.420) \) between sheep occupying north and south units of BNP. This indicated that movement and interbreeding were occurring between these 2 populations in 1992–2004; therefore, bighorn sheep samples were pooled by capture years (e.g., 1992, 1996, 1998, Adult04). I compared \( F_{st} \)-values between capture years and the greatest substructure occurred between historic and Adult04 (Table 16). Historic bighorn sheep had the lowest \( N_a \) and \( N_{ea} \) whereas translocated bighorn sheep had the highest \( N_a \) and \( N_{ea} \) (Table 17, Fig. 12). Polymorphic loci were lowest in historic samples followed Adult04 (Table 17). Observed and expected heterozygosity was lowest in historic bighorn and greatest in Off0506 (Table 17, Fig. 13).

<table>
<thead>
<tr>
<th>Location</th>
<th>1992</th>
<th>1996</th>
<th>1998</th>
<th>Adult05</th>
<th>NMIntro</th>
<th>Off0506</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historic</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historic</td>
<td>0.221</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historic</td>
<td>0.223</td>
<td>0.019</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historic</td>
<td>0.233</td>
<td>0.012</td>
<td>0.029</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historic</td>
<td>0.287</td>
<td>0.059</td>
<td>0.053</td>
<td>0.073</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Adult05</td>
<td>0.263</td>
<td>0.172</td>
<td>0.203</td>
<td>0.200</td>
<td>0.258</td>
<td>0.000</td>
</tr>
<tr>
<td>Adult05</td>
<td>0.212</td>
<td>0.068</td>
<td>0.093</td>
<td>0.090</td>
<td>0.127</td>
<td>0.051</td>
</tr>
</tbody>
</table>

The $F_{is}$-statistic is a measure of the departure from Hardy-Weinberg proportions with local subpopulations (Allendorf and Luikart 2007). Negative $F_{is}$ values indicate an excess of heterozygotes (i.e., deficit of homozygotes), whereas positive values indicate a deficit of heterozygotes (i.e., an excess of homozygotes) (Allendorf and Luikart 2007). A significant ($P < 0.001$) excess of heterozygotes was observed in the Off0506, but remaining populations did not differ from Hardy-Weinberg proportions (Table 17).

Based on all loci of resident bighorn sheep, rate of expected loss of heterozygosity was 9.8% from 1992–1998 and 5.05% from 1998–2004, with a total decrease of 1.1% per year from 1992–2004 (Fig. 14). Declines in genetic parameters followed a similar trend observed in population size (Fig. 15).

**DISCUSSION**

Genetic variability can be described by allelic variation and heterozygosity (Whitaker et al. 2004). Allelic variability functions to allow adaptation to local environments or
Figure 12. Effective and average number of alleles of historic (<1925), resident (1992–2004) and translocated (2004) bighorn sheep and their offspring (2005–2006) at Badlands National Park, South Dakota, USA.


<table>
<thead>
<tr>
<th>Pop.</th>
<th>Min.</th>
<th>N_{ea}</th>
<th>N_{a}</th>
<th>I</th>
<th>H_{o}</th>
<th>H_{e}</th>
<th>Poly. loci</th>
<th>F_{is}</th>
<th>F_{is} P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historic</td>
<td>n/a</td>
<td>2.00</td>
<td>1.75</td>
<td>0.61</td>
<td>0.32</td>
<td>0.39</td>
<td>12</td>
<td>0.14</td>
<td>0.99</td>
</tr>
<tr>
<td>1992</td>
<td>83–101</td>
<td>4.20</td>
<td>2.23</td>
<td>0.96</td>
<td>0.51</td>
<td>0.52</td>
<td>15</td>
<td>0.03</td>
<td>0.99</td>
</tr>
<tr>
<td>1996</td>
<td>71–72</td>
<td>3.20</td>
<td>2.10</td>
<td>0.83</td>
<td>0.54</td>
<td>0.49</td>
<td>15</td>
<td>-0.11</td>
<td>0.34</td>
</tr>
<tr>
<td>1998</td>
<td>66</td>
<td>3.20</td>
<td>2.03</td>
<td>0.82</td>
<td>0.50</td>
<td>0.47</td>
<td>15</td>
<td>-0.04</td>
<td>0.33</td>
</tr>
<tr>
<td>Adult04</td>
<td>67</td>
<td>2.20</td>
<td>1.66</td>
<td>0.59</td>
<td>0.47</td>
<td>0.37</td>
<td>14</td>
<td>-0.22</td>
<td>0.50</td>
</tr>
<tr>
<td>NMIntro</td>
<td>91</td>
<td>4.93</td>
<td>3.20</td>
<td>1.23</td>
<td>0.67</td>
<td>0.63</td>
<td>15</td>
<td>-0.02</td>
<td>0.46</td>
</tr>
<tr>
<td>Off0506</td>
<td>69–89</td>
<td>4.40</td>
<td>3.11</td>
<td>1.22</td>
<td>0.83</td>
<td>0.65</td>
<td>15</td>
<td>-0.27</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

N_{a} = \bar{x} number of alleles per locus, \ N_{ea} = number of effective alleles, I = information index, H_{o} = observed heterozygosity, H_{e} = expected heterozygosity, F = fixation index, F_{is} = Hardy-Weinberg multisample score test for heterozygote excess (Rousset and Raymond 1995)

\[
y = -0.0127x + 0.5479 \\
R^2 = 0.9646
\]

Figure 14. Expected heterozygosity of resident bighorn sheep prior to an augmentation at Badlands National Park, South Dakota, USA (1992–2004).
environmental stochasticity, whereas heterozygosity allows retrospective evaluation of recent breeding activity (Whitaker et al. 2004). In this study, I documented that historic bighorn sheep had the lowest $N_e$, polymorphic loci, and $H_o$. The number of polymorphic loci was low (i.e., 12) compared with other time periods (i.e., 14–15) evaluated. This may have been a result of the small sample size ($n = 3$) because as sample size increases the more likely rare alleles will be detected (Allendorf and Luikart 2007). Other genetic parameters such as $N_a$ and $H_e$ are adjusted for or not influenced by sample size (Allendorf and Luikart 2007). Expected heterozygosity and $N_a$ of historic bighorn sheep were low compared with other time periods, and the $F_{is}$, although not significant, was negative indicating potential heterozygote deficit due to inbreeding. Lack of genetic variability
and increased inbreeding may result in decreased growth, survival, fertility, development rate, and adaptive ability while increasing susceptibility to epizootics (Allendorf and Luikart 2007). Low heterozygosity and allelic diversity of historic populations may have made bighorn sheep more susceptible to the diseases of domestic sheep and, therefore, may have contributed to the local extinctions of this ecotype throughout its range. Further analysis of the loci in candidate genes (i.e., ADCYAP1, TCRG4, MMP9, OLADRBps) may provide more insight into proximate cause of the extirpation of the Audubon’s ecotype.

Ramey et al. (2000) used the same genetic and demographic data for BNP bighorn sheep collected in 1992 that I used. They determined that bighorn sheep at BNP had undergone a severe population bottleneck ($N_e < 10$) at founding, but it was not apparent that the bottleneck was deleterious to the BNP population (Ramey et al. 2000). Ramey et al. (2000) speculated that environmental factors (e.g., disease and predation) and demographic stochasticity may have obscured the population-level effects of the genetic bottleneck (Ramey et al. 2000). Based on my findings, genetic variability of resident bighorn sheep at BNP declined from the time of Ramey et al.’s (2000) study in 1992 to their pre-augmentation level in 2004 (i.e., Adult04). Inbreeding typically results in reduced genetic variability, which influences fitness (Hogg et al. 2006) and reduces phenotypic traits important for fitness (Fitzsimmons et al. 1995). Horn size is an important phenotypic trait in bighorn sheep because large horned individuals have increased access to estrous females (Geist 1971, Fitzsimmons et al. 1995). Although small horn size has been correlated with low genetic variability (Fitzsimmons et al. 1995).
most males collected from BNP that were \( \geq 7.5 \) years of age have met minimum entry size for Boone and Crockett (i.e., 175) (Table 18).

Table 18. Age (years), horn length (inches), basal circumference (inches), and Boone and Crockett scores of males collected at Badlands National Park, South Dakota, USA (1994–2007).

<table>
<thead>
<tr>
<th>Year</th>
<th>Age</th>
<th>Horn length (right)</th>
<th>Horn length (left)</th>
<th>Base circ. (right)</th>
<th>Base circ. (left)</th>
<th>B &amp; C Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>13.5</td>
<td>39.50</td>
<td>40.50</td>
<td>14.50</td>
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Adult04 had the lowest \( N_a \), \( N_{ea} \), polymorphic loci, \( H_o \), and \( H_e \) compared with other recent populations in BNP. Expected heterozygosity and \( N_a \) of Adult04 bighorns were similar to 5 populations of California bighorns in Oregon (Whitaker et al. 2004).

The Oregon populations were similar to the BNP population with regard to founding size, time since reintroduction, and relative isolation, but 3 of the populations had been augmented within the past 2 decades (Whitaker et al. 2004). Like the BNP population, bighorn sheep at the National Bison Range had undergone a population bottleneck at founding but was genetically isolated for 23 years more than the BNP population (Forbes et al. 1995). Genetic variability of bighorn sheep on the Bison Range was extremely low relative to other populations of \( O\nu\nuis \) with \( H_e = 0.44 \) and \( N_a = 2.2 \). The \( H_e \) and \( N_a \) of the
Adult04 samples were comparable to the historic samples at BNP and would therefore be considered low compared with other populations of *Ovis*.

Dispersal, coupled with substructure of populations maintains genetic diversity (Bleich et al. 1990). The South Unit of BNP is approximately 20 km from the Pinnacles subpopulation (i.e., the site of the 1964 and 2004 translocations) and maintains a stable but small (e.g., 12–30 individuals) population of bighorn sheep. Although origin of the bighorn sheep in the South Unit was unknown, local ranchers speculated that occupation in the South Unit occurred in 1981 when individuals from the North Unit of BNP naturally colonized the area (Badlands National Park Resource Management Plan and Environmental Assessment 1984). Radio-collared males in the 1990’s had been observed moving between these 2 populations but the extent of interherd movements was relatively unknown (E. Childers, Badlands National Park, personal communications, September 2004). Based on the $F_{st}$, movement between the North and South Units of BNP had occurred relatively frequently (i.e., $\approx 11.7$ migrants/generation) between 1992 and 2004. Although relatively low levels of migration are necessary to prevent loss of genetic diversity in small populations (Bleich et al. 1990), temporal distance between BNP herds was not sufficient to cause genetic divergence. Three F1 were observed 32 km southeast of the south unit population in 2006 (Chapter 1), but these individuals were not observed with the South Unit population. The North and South Unit herds may have become spatially isolated if migration patterns were abandoned in recent years. Continued monitoring of genetic parameters and movements of radio-collared bighorn is necessary to determine if interherd connectivity is maintained between the North and South Unit. If
the South Unit herd has become genetically isolated, translocation or human assisted dispersal may be necessary to maintain genetic viability in the South Unit.

Genetic rescue of small inbred populations can occur when immigration (or augmentation) alleviates inbreeding depression and increases population fitness. (Tallmon et al. 2004). Increases in fitness (i.e., heterosis) may result from either the masking of deleterious, recessive alleles that have achieved high frequencies or through interbreeding between residents and immigrants (or translocated individuals) resulting in highly heterozygous offspring (Tallmon et al. 2004). In this study, augmentation increased $H_o$, $H_e$, $N_a$, and $N_ca$ of F1 bighorn sheep at BNP resulting in a $H_e$ and $H_o$ greater than those reported for large, native herds in Canada (0.585) and the United States (0.549–0.591) (Forbes et al. 1995). Hogg et al. (2006) also observed rapid restoration of genetic variation due to an admixture of outbred populations of bighorn sheep with $H_o$ increasing from 0.50 to 0.68 following augmentation. Heterozygosity results in an increase in the overall fitness of the local population and may increase population growth (Tallmon et al. 2004). The results of restoration at the Bison Range resulted in demographic recovery at the individual (e.g., increased individual fitness) and population (e.g., increased population growth and size) level (Hogg et al. 2006). Similar changes in fitness and population growth may be expected at BNP.

Augmentation with genetically divergent individuals also results in outbreeding depression causing a reduction in population fitness (Tallmon et al. 2004). Outbreeding depression occurs when local alleles, which contribute to fitness, are diluted resulting in a decrease in local adaptation (Tallmon et al. 2004). Although high heterozygosity may be
observed in F1, in subsequent generations positive epistatic interactions may be disrupted at different loci reducing intrinsic coadaptation, and resulting in reduced fitness (i.e., outbreeding depression) of F2s and following generations (Tallmon et al. 2004). Heterozygosity and associated heterosis peaks in F1 and declines in subsequent generations (Tallmon et al. 2004); therefore, the significant $F_{is}$ observed in BNP F1 was expected. Monitoring of population parameters (e.g., growth rates, genetic composition) of subsequent generations will determine if augmentation of BNP bighorn sheep provided a genetic rescue or resulted in population declines due to outbreeding depression (Tallmon et al. 2004).

**LITERATURE CITED**


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CHAPTER 5

MANAGEMENT IMPLICATIONS
The objective of the 2004 augmentation of bighorn sheep from Wheeler Peak, New Mexico to Badlands National Park (BNP) was to restore the genetic diversity and increase population numbers of bighorn sheep in BNP. Based on the genetic and population parameters evaluated in this study, the 2004 translocation was successful. Data collected in this study will be useful to ascertain the population ecology of low-elevation and translocated bighorn sheep herds and will serve as an aid to the restoration of bighorn sheep throughout their range. The following management and research recommendations are suggested from this study.

Although lamb:ewe ratios of bighorn sheep declined following translocation, the number of lambs produced from 2005–2007 was sufficient (>25:100 lambs:ewes) for population growth to occur (Douglas and Leslie 1999). Furthermore, high survivorship of translocated individuals, low mortality of lambs, and relative absence of lungworms and disease from necropsied yearlings indicated that disease and predation of adults were not influencing the bighorn sheep population at BNP. Lamb production by 1- and 2-year-old females indicated that female bighorn sheep were sustained on a high nutritional plane during this study; therefore, density-dependent effects, such as reduced range conditions did not influence reproductive performance (Wehausen 1984). To ascertain what factors are contributing to the declining lamb:ewe ratio, I recommend that research efforts focus on determining: 1) pregnancy rates of all ewes through analysis of fecal metabolites (Stoops et al. 1999), 2) stress levels through the analysis of fecal glucocorticoids (Millspaugh et al. 2001), and 3) predation rates of neonate lambs through coyote and bobcat scat analysis during the lambing period (i.e., May 1–June 15).
The primary factor influencing population growth during this study was poor yearling recruitment due to long-distance movements. The proximate and ultimate cause of these movements from BNP by male and female bighorn sheep was unknown. I recommend that lambs be radio-marked at < 12 months-of-age and intensely monitored from 1 May to 30 June. If individuals of this age class continue to move outside of natal or maternal home-ranges, cooperative efforts between the NPS and the South Dakota Department of Game, Fish and Parks (SDGFP) should be made to capture yearlings prior to contact with domestic sheep. If yearlings are captured, individuals may be translocated to other areas identified in the bighorn sheep habitat model in BNP (e.g., Cedar Pass, Cedar Butte). Subsequent monitoring following translocation is recommended to evaluate the outcome of translocation (Douglas and Leslie 1999). Translocation to other areas in South Dakota (e.g., Black Hills) could occur but consideration must be given to group vigilance, predation risk, and disease transmission (Mooring et al. 2004).

Badlands National Park and SDGFP should work cooperatively to develop a management plan in which a buffer distance around domestic sheep herds is defined. All bighorn sheep occurring within this buffer should be euthanized as a preventative measure to curtail disease transmission to other bighorn sheep populations (Desert Bighorn Council 1990). If yearling dispersal continues to occur as an annual event, human-assisted translocation of individuals < 12 months of age to other areas of BNP or other suitable habitat in South Dakota may be a viable alternative. Dispersing bighorn sheep from BNP travel across a large number of political boundaries (e.g., state, federal,
reservation, and private lands); therefore, interagency communication and cooperation will be essential to scrutinize the potential management alternatives.

I recommend that long-term objectives of bighorn sheep research and management at BNP include continual visual relocations of translocated bighorn sheep and their offspring. These data will allow biologists to examine survivorship, annual variability in home-range size, shifts in habitat selection, interherd movements, and factors contributing to changes in habitat use. Due to their proximity to high human-use areas, numerous observations have been made of Park visitors harassing (e.g., chasing, feeding, throwing objects) translocated bighorn sheep. Peak visitation at BNP occurs in July–August when females are already stressed by lactational demands. Objectives for all Divisions (e.g., Resource Management, Resource Education, Resource Protection) within BNP should focus on strategies to minimize deleterious effects of anthropogenic activity (Bleich et al. 1994, Frid and Dill 2002) on bighorn sheep while still maintaining nonconsumptive uses of the species for Park visitors (Geist 1975). Most visitors do not have malicious intentions in their response to wildlife at BNP but rather lack the appropriate guidance on acceptable behaviors. Visitors need to be educated in methods to reduce their impact on bighorn sheep and other wildlife species. I recommend that Park visitors be provided with literature on acceptable behavior around wildlife. In this literature, harassment and feeding of wildlife along with the penalties of violation need to be clearly defined. Although domestic dogs are not allowed in the wilderness at BNP, dogs are allowed in all other areas of the park if leashed. Because of the behavioral response domestic dogs elicit in bighorn sheep (Pelletier 2006), I recommend that BNP
should establish designated areas where visitors may remove their dogs from their vehicles. These areas should not be located where bighorn sheep populations are established (e.g., Pinnacles Overlook, Hay Butte Overlook, Sage Creek Wilderness Overlook, Doors and Windows Overlooks, Fossil Trail Exhibit, Cliff Shelf Overlook, and Cedar Butte). Future research at BNP should focus on evaluating long-term effects of human activity on stress levels, home-range size, and habitat selection of the translocated bighorn sheep utilizing these habitats.

Based on the bighorn sheep habitat model, it appears that there is adequate suitable habitat in the BNP ecosystem to establish additional herds. Some of the largest habitat patches occur in the South Unit and are currently unoccupied by bighorn sheep (e.g., Stronghold, Palmer Creek, Indian Creek). The Pine Ridge Reservation currently enforces a “no domestic sheep” policy (Trudy Ecoffey, Oglala Sioux Parks and Recreation Authority, personal communication) throughout Shannon County. This policy in conjunction with large patches of suitable habitat bode well for translocation success. Furthermore, reestablishing herds in these areas may aid in reconnecting the BNP population with other populations in South Dakota (e.g., the Black Hills) and western Nebraska (e.g., Chadron State Park, Scottsbluff) creating a viable metapopulation of prairie bighorn sheep. If interherd movements are reestablished, it will aid in the long-term genetic viability of these populations (Bleich et al. 1990). I recommend that research be conducted to ascertain the nutritional carrying capacity of bighorn sheep and other herbivores to aid in restoration efforts (DeYoung et al. 2000). Data on diet quality, diet composition, and dietary overlap of bighorn sheep and other native (e.g., bison, mule
deer, prairie dogs, pronghorn antelope) and non-native herbivores (e.g., cattle) are necessary to evaluate the potential of these sites for bighorn sheep restoration (DeYoung et al. 2000). Furthermore, availability of water and suitable lambing range should be vigorously evaluated (Zeigenfuss et al. 2000).

Based on the genetic parameters evaluated in this study, I conclude that the augmentation was effective at increasing the genetic diversity and short-term viability of the bighorn sheep population at Badlands National Park. Concern is warranted that outbreeding depression may occur in the second generation offspring (F2) and subsequent generations (Tallmon et al. 2004). I recommend that non-invasive genetic samples (i.e., feces) (Wehausen et al. 2004) are collected from F2s and subsequent generations in addition to samples from resident bighorn sheep in the Pinnacles, Cedar Pass, and South Unit populations to evaluate outbreeding depression. These data, in addition to data on population size and survivorship, will provide managers with insight on individual and population fitness (Tallmon et al. 2004). Furthermore, the Cedar Pass and South Unit herds need to be genetically monitored to determine if interherd movement from Pinnacles is still occurring. If these populations become genetically isolated additional translocations from the Pinnacles subpopulation or another source herd is warranted. Long-term viability of bighorn sheep at BNP does not appear to be limited by genetic diversity but rather by population size. Management objectives should focus on increasing the total BNP population size to \( \geq 150 \) individuals as recommended by Fitzsimmons and Buskirk (1992). Additional translocations into BNP, or other areas
identified by the habitat model, may be necessary if population recruitment does not increase.

At this time, disease does not appear to be a threat to the viability of the BNP populations because survivorship of all ages classes was high and no clinical signs of disease were apparent in the population. Many diseases that threaten other bighorn sheep populations throughout the West such as contagious echthyma, psoroptic scabies, chronic sinusitis, paratuberculosis, or mandibular osteomyelitis (Bunch et al. 1999) appear to be absent from the BNP population. History of disease in potential source herds needs to be evaluated to reduce introduction of diseases in the BNP herd. Furthermore, BNP, the U.S. Forest Service, and the SDGFP should work cooperatively to maintain separation of domestic sheep and bighorn sheep herds throughout South Dakota to reduce population die-offs from *Pastuerella* spp. epizootics (Bunch et al. 1999).

**LITERATURE CITED**


APPENDICES
Appendix 1. Lamb production of translocated female bighorn sheep in 2005–2007, Badlands National Park, South Dakota, USA.

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<td>--</td>
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2006

0 = not observed with a lamb, 1 = observed with a lamb, 2 = observed with a lamb on lambing range but not on nursery range, -- = individual was not alive during the period.

Appendix 2. Translocated ewe 95% and 50% home-range estimates (km²) at Badlands National Park, 29 October 2004–August 2006.

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$^1$ Home-range estimator separated into 2 polygons at 100% h-ref, $^2$ Herd home-range calculated with all translocated females except 36D and 43D, A= adaptive kernel home-range estimator, F = fixed kernel home-range estimator, MCP = Minimum convex polygon home-range estimator.

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A = adaptive kernel home-range estimator, F = fixed kernel home-range estimator, MCP = Minimum convex polygon home-range estimator
Appendix 4. Translocated ewe 95% and 50% home-range estimates (km$^2$) in year 1 at Badlands National Park, South Dakota, 28 October 2004–28 July 2005.

<table>
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A = adaptive kernel home-range estimator, F = fixed kernel home-range estimator, MCP = Minimum convex polygon home-range estimator.
Appendix 5. Translocated ewe 95% and 50% home-range estimates (km$^2$) in year 2 at Badlands National Park, South Dakota, 29 October 2005–28 July 2006.

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$^1$ Home-range estimator separated into 2 polygons at 100% h-ref, A = adaptive kernel home-range estimator, F = fixed kernel home-range estimator, MCP = Minimum convex polygon home-range estimator