Movement and resource selection of recolonizing bighorn sheep in western Montana

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The University of Montana
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MOVEMENT AND RESOURCE SELECTION OF RECOLONIZING BIGHORN SHEEP IN WESTERN MONTANA

by

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Chairperson

Dean, Graduate School

Date
Abstract:

Three herds of bighorn sheep (*Ovis canadensis*) recently colonized unoccupied habitat in western Montana. Natural recolonization by bighorn sheep has been rare, and the status and movements of these sheep have implications for future bighorn conservation in the state. I used radio-telemetry to study the resource selection and movements of sheep at each site.

Sheep within each herd lacked independence in their movements. Resource selection occurred at the level of the herd, not the individual, so I pooled our location data within herds. I used GIS to quantify many habitat variables within sheep home ranges. One particular variable, horizontal visibility, is not easily measured by GIS. I measured horizontal visibility in the field at used and paired available sites 200 m away and did not detect significant selection at this scale. I also used multiple regression to model horizontal visibility based on other variables in the GIS. All included explanatory variables were important in predicting horizontal visibility, though much unexplained variation remained. I did not include horizontal visibility in my resource selection modeling.

I used logistic regression and resource selection function (RSF) methods in a GIS to generate RSF models for each herd of sheep. Initial evaluation of models by resubstituting the same data revealed excellent fit and predictive accuracy ($P \leq 0.002$). However, testing models across sites with independent testing data gave mixed results, and in many cases poor fit ($P = 0.001 - 0.960$). Increasing slopes and decreasing distances to escape terrain were important in most models, but site-specific variation caused inconsistent relationships for other explanatory variables.

Autumn lamb:ewe ratios for each herd were relatively high. Disease did not appear to be a major source of mortality, but the potential for contact with domestic sheep is high. I detected large, migratory movements by rams in all 3 herds, and connectivity with another bighorn herd in at least 1 case. Ewes remained in local home ranges; I believe these are independent herds rather than range expansions of source populations.
ACKNOWLEDGEMENTS

This project has been a collaboration at all levels, and I am very grateful to many people and organizations. Funding has come from partnership between The University of Montana, Montana Department of Fish, Wildlife and Parks (FWP), The Bitterroot National Forest, The Bureau of Land Management, The Boone and Crockett Wildlife Conservation Program, Plum Creek Timber Company, The Welder Wildlife Foundation, The Five Valleys Chapter and National Headquarters of Safari Club International, and The Montana Chapter of the Foundation for North American Wild Sheep. I owe an enormous thank you to everybody involved with these organizations for their faith and support in me and the project.

I enjoyed many conversations with John Firebaugh, Bob Henderson, and Mike Thompson of FWP Region 2 in between trips to the field. I valued their experience with the region’s land and wildlife and was always excited to share stories with such nice people. I also thank Dr. Jack Hogg for his time in the field and office. It was an honor to interact with somebody who has developed such knowledge and respect for bighorn sheep. In addition to John Firebaugh and Jack Hogg, my academic committee consisted of Dr.’s Kerry Foresman, Jack Ward Thomas, and Lorin Hicks. They provided new insight into the perspectives of studying resource selection and bighorn sheep. Most of all, I owe an enormous thank you to my main advisor and mentor, Dr. Daniel H. Pletscher. Dan’s dedication both to me and my project were invaluable, and I will be forever grateful for his guidance throughout it all. Thank you Dan. Equally patient and supportive was our Wildlife Biology administrator Jeanne Franz, who was always there to keep me on track and in line. I am also thankful to have been surrounded by great fellow graduate students, who taught me as much as anybody about wildlife biology, science, and life.

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This study would never have been possible without the unquestioned support and cooperation of many private landowners throughout the study area. I would like to especially thank Larry and Peggy Trexler, Bob and Linda Curren and the entire Rippingale family, Tom and Vicki at the Rock Creek Ranch, everybody at the Bearmouth Chalet, Fred Weaver, Frank and Barbara Renfro, Tom Gilbert, and the McGillis family. I have come to know their places as another home these past two years, and I am very grateful to everybody for sharing them with me.
I give my most sincere thanks to all my amazing friends and family, but especially my parents, William and JoEllyn DeCesare. I have discussed practically every step of the way with my parents and their love, support, and guidance is beyond compare. Thank You.

Finally, I have to thank these areas’ incredible bighorn sheep. The past 2 years in the field have spawned some of the most powerful moments of my life. It has been an enormous privilege to share so much time and energy with these animals, and I am grateful to them for teaching me so much about themselves and natural places. I hope my research will contribute to the conservation of these animals and their natural homes into perpetuity.
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Chapter 1. Introduction

Bighorn sheep (*Ovis canadensis*) suffered a dramatic population decline and reduction in distribution during the latter part of the 19th century. Buechner (1960) estimated that 15,000 to 20,000 remained in the contiguous U.S. in 1960. Decades of intensive restoration brought 1991 population estimates up to 49,000 in the lower 48 states (Valdez and Krausman 1999). Sheep were perceived as poor dispersers with strong site fidelity (Geist 1970, 1971) so conservation efforts focused on artificially reintroducing sheep into unoccupied habitat (Hansen et al. 1980). The resultant network of new, isolated populations remains vulnerable to factors such as genetic isolation and disease outbreaks (DeForge et al. 1979, Sausman 1984, Fitzsimmons et al. 1995, Bunch et al. 1999). Costly reintroductions and supplemental transplants are still used to augment sheep populations, and they remain a heavily managed species.

Several well established herds of Rocky Mountain bighorn sheep (*O. c. canadensis*) currently exist in western Montana. During the early 1980’s bighorn sheep began to appear in 3 previously unoccupied areas. There appeared to be self-sustaining herds in these new areas by the mid 1990’s, though little was known about their population sizes, potential connectivity to other nearby herds, or habitat selection.

The appearance of 3 naturally colonized herds in western Montana carried many important implications. It was possible that sheep were revealing dispersal and colonization abilities that once made them so widespread across the western U.S. (Geist 1971). These 3 herds might represent the beginning of an exciting natural recolonization of Montana’s suitable habitat. This accomplishes the same thing as expensive translocation management, but, even better, lets the animal decide what habitat is
suitable. However, dispersal and connectivity among populations of sheep also create a fast and dangerous path for the spread of disease. Bighorn sheep are very susceptible to pasteurellosis and pneumonia commonly associated with domestic sheep (*Ovis aries*); populations of over 250 have been reduced to 0 in under 10 years after pneumonia outbreaks (Foreyt and Jessup 1982, Jessup 1985, Technical Staff of the Desert Bighorn Council 1990, Bunch et al. 1999).

We captured and radio-collared bighorn sheep at each of these 3 sites in March, 2001, to assess their distribution, movements, and habitat selection. This thesis presents the results of 18 months of consecutive field work relocating and monitoring radio-collared animals. I had 2 primary objectives: 1) quantify and compare resource selection among these 3 herds using resource selection function (RSF) methods (Manly et al. 1993), and 2) monitor the distribution and movements of these animals to assess their potential for connectivity with other well-established herds of bighorn sheep.

Chapters 2, 3, and 4 are separate manuscripts intended for publication, but combined, they are all steps towards quantifying bighorn sheep resource selection. In Chapter 2, I used a nearest-neighbor test to assess the degree of independence in movements between radio-collared individuals. This addresses whether radio-collared animals are acting as separate individuals or as a single herd. In Chapter 3, I isolated a single habitat variable, horizontal visibility, found to be important in past evaluations of bighorn sheep habitat. I tested for selection by sheep of areas with higher horizontal visibility than randomly expected, and then attempted to model this variable using several predictor variables easily quantified with GIS. In Chapter 4 I used logistic regression and RSFs to model and predict bighorn habitat use within and across these 3 sites. This
chapter evaluates the application of site-specific RSF models, and examines the degree of variation between 3 recolonized bighorn sheep habitats.

Chapter 5 presents many other data concerning these 3 herds that may be useful for future management. I discuss their history, health, abundance, mortality, movements, and home ranges. In Chapter 6, I make some final conclusions for future research and management. This research was all collaborative, and for Chapters 2, 3, 4, and 5 I have used ‘we’ instead of ‘I’ to include future co-authors. I directed all of the field work, data analysis, and writing and take full responsibility for any errors within this thesis.

LITERATURE CITED


Chapter 2. The assumption of spatial independence in resource selection by bighorn sheep

Abstract: A common assumption in the analysis of resource selection data is that marked individuals move and select resources independently. This assumption can significantly affect results of habitat selection analysis if animals are highly social or territorial. In the case of bighorn sheep (Ovis canadensis), social groups are prevalent throughout the year, raising concerns about the independence of marked individuals. Prior methods for testing spatial independence do not adequately assess the spatial and temporal nature of relocation data. Nearest-neighbor analysis has been used to test avoidance behavior by carnivores. We used this method and data from 3 small herds of bighorn sheep in western Montana to detect dependency in location data from marked animals. In most cases, marked ewes within each study area were not independent of each other. This issue can be important in a posteriori analysis and interpretation of data, as well a priori consideration of necessary sample sizes.

INTRODUCTION

Each marked animal often represents 1 sample in studies of wildlife ecology. The resultant sample size of animals can strongly affect results for many types of analyses. One key assumption when making inferences from many individuals in a study area is their spatial independence, and animals that attract or avoid each other can violate this assumption. This is an issue both a priori and a posteriori in a study. Before incurring the often significant costs of capturing or monitoring many animals in an area, the
question of spatial independence should be raised. This might avoid a frustrating *posteriori* discovery that 20 sampled animals are in fact acting as 1. Consideration of this issue is important, because an analysis of dependent animals can lead to inflated sample sizes and biased results.

A variety of analytic methods are available within the broad field of resource selection, including chi-squared goodness-of-fit tests (Neu et al. 1974, Byers et al. 1984), ranking methods (Johnson 1980), compositional analysis (Aebischer et al. 1993), and general linear models (Manly et al. 1993). Each of these methods has its own set of assumptions, but they all assume that sampled animals select resources independently. Spatial independence is demanded across all forms of resource selection analysis. We consider this assumption when dealing with relocation data from radio-telemetry. One can use a set of “simultaneous” locations for 2 animals to assess their dependence over space and time. The biologist determines the maximum time interval between locations to consider them simultaneous, but simultaneous data are required.

We are not the first to discuss or quantify spatial independence; the issue has been prevalent for a long time, and many different techniques have been used to assess it. Cole’s (1949) coefficient of association has been used sporadically in the study of bighorn sheep to coarsely assess group cohesion (Brown 1974, Leslie and Douglas 1979, Elenowitz 1984, Ebert 1993). This is a simple formula, \(2c / (a+b)\), where \(a\) is the number of times animal A was observed, \(b\) the number of times animal B was observed, and \(c\) the number of times animals A and B were observed together. Animals always together would score a CA of 1, while animals never together would score a 0. This is an
intuitive, but fairly crude measure, because it ignores most of the spatial information in relocation data.

The overlapping of home ranges has also been used to detect avoidance or attraction between individuals (Adams and Davis 1967, Jorgensen 1968). A more sophisticated method proposed by Minta (1992) considered the use or avoidance of this overlap area by 1 animal while the neighboring animal was either in or out of the same area. The simplification of relocations into home ranges involves the loss of information, and it may be preferable to consider locations without such reduction.

Millspaugh et al. (1998) suggested a chi-squared goodness-of-fit test where 2 animals’ preferences for different habitat types are used to calculate how often they might be expected together. This is compared to how often they were observed together. While their intention to shift the focus from statistical independence to biological independence is commendable, this test is over-simplified and succumbs to the very biases it aims to test – it is based on inferred habitat preferences that may already be biased by lack of independence.

Dasgupta and Alldredge (2000) created a dependency parameter, p, which they used to update the Neu et al. (1974) method of measuring resource selection. Their method tests for dependence, and includes it as a parameter in calculating the chi-square test statistic. This method is limited to chi-square goodness-of-fit analyses, and their suggested dependency parameter assumes that, in absence of dependency between animals, they would be distributed randomly across the landscape. This is rarely the case. Ecologists using other resource selection analyses such as compositional analysis or logistic regression modeling might find this method of limited use.
The above methods test how often animals are detected in the same place at the same time compared to random expectations. No distinctions are made among animals that are not together; 2 animals 500 m apart are treated the same as 2 animals 5000 m apart. This creates arbitrary cut-off values for defining how close the animals must be to be “together.” A more robust test should maintain the continuous nature of these spatial relationships. In this paper, we present an alternative method for quantifying spatial independence with relocation data that has been used to detect avoidance behavior in carnivores (Keenan 1981, Major and Sherburne 1987, White et al. 1994, Arjo 1999). The modified nearest-neighbor technique tests dependence between 2 animals as a function of the distance between them, and we use it to detect dependency in radio-telemetry data from bighorn sheep. This method allows researchers to explicitly test relocation data for spatial independence before carrying out further analyses.

METHODS

Data Collection

In March, 2001, we captured and radio-collared 16 adult female Rocky Mountain bighorn sheep (O. c. canadensis) at 3 sites using a net-gun from a helicopter (Krausman et al. 1985). We attempted to capture animals from different subgroups within each herd, and ended with 2 (Bearmouth), 7 (Garrison) and 7 (Skalkaho) radio-collared animals per site. Between March, 2001 and August, 2002, we collected 1,034 locations for these 16 ewes. Locations for the same animal were collected a minimum of 3 days apart to ensure suitable temporal independence within an individual set of locations (Swihart and Slade 1985, Swihart et al. 1988, Ebert 1993, McNay et al. 1994). Locations were sorted by
herd and season, so analyses were done for a given pair of ewes of the same herd during
the same season. Biologically meaningful seasons were selected by finding noticeable
shifts in habitat use by ewes during the transitional periods. For example, a notable shift
towards rocky escape terrain marked the beginning of lambing season each spring.
Roughly, the lambing season lasted from early May through late July, the fall season
from early August through late November, and the winter season from early December
through late April. A minimum of 10 pairs of simultaneous locations was required for
analysis for each season (Arjo 1999).

**The Modified Nearest-Neighbor Test**

The nearest-neighbor test detects whether 2 animals are randomly located
throughout the landscape in relation to one another. Significant results would come from
animals that are closer together or further apart than would be expected from random
association. It begins with a set of “simultaneous” locations for 2 animals over time. For
our purposes, “simultaneous” meant the 2 animals were located on the same day, roughly
within an 8 hour period. A distribution of distances is created by measuring the distance
between the 2 animals for each pair of simultaneous locations. On a day when the 2
animals were located together, this distance is essentially 0.

Another distribution of distances is created by randomly pairing the same set of
locations without considering time. For example, animal A’s location on day 3 might be
paired with animal B’s location on day 12. These random pairs are selected with
replacement; we used a standard sample size of 500 randomly selected pairs to get a
distribution of 500 distances. The end result is 2 distributions of distances: 1) distances
between simultaneous locations of two ewes, and 2) distances between the same set of
locations randomly paired with replacement. We used the non-parametric Mann-Whitney U to test for differences between these 2 distributions. The effect size, or average difference between the 2 distributions, is also important in considering biological significance.

We applied this test to ewes from 3 herds with sample sizes of 2, 7, and 6 radio-collared ewes. This resulted in 1, 21, and 15 possible ewe-pairs, respectively. We considered the distribution and range of effect sizes and p-values to assess the degree of independence at the herd level.

RESULTS

We found a lack of independence between bighorn sheep ewes within all 3 herds (Table 1). All effect sizes were positive, indicating that randomly paired locations were always further apart than simultaneous locations. A single ewe-pair was analyzed for the Bearmouth herd; effect sizes were large, and p-values were low across seasons. This suggests dependency in the movements and resource selection of these 2 ewes. Twenty-one combinations of ewe-pairs per season from the Garrison herd also showed large effect sizes and low significance values; it is evident that these 7 radio-collared ewes lacked independence in their movements. Fifteen possible combinations of ewe-pairs per season in the Skalkaho herd produced a wider range of p-values, though effect sizes were consistently positive. Each ewe was dependent on at least 1 other ewe per season, and we found no evidence of segregation between groups of ewes. We concluded that these Skalkaho sheep lacked independence in their movements and should be analyzed as a herd instead of as individuals.
Table 1. Median effect sizes (meters) and Mann-Whitney U Test probability values for modified nearest-neighbor tests of spatial independence between bighorn sheep ewes of Bearmouth (n=2), Garrison (n=7), and Skalkaho (n=6), 2000-2001. All possible ewe-pairs within each herd were tested. Effect size = (mean distance between randomly paired locations – mean distance between simultaneous locations).

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<th>fall</th>
<th>winter</th>
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<td>Median effect size</td>
<td>1153</td>
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<tr>
<td></td>
<td>( P )</td>
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<td>Garrison (21 ewe-pairs)</td>
<td>Median effect size</td>
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<td>977</td>
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<td></td>
<td>( P )</td>
<td>&lt; 0.001 - 0.012</td>
<td>&lt; 0.001 - 0.003</td>
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<tr>
<td>Skalkaho (15 ewe-pairs)</td>
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<td>224</td>
</tr>
<tr>
<td></td>
<td>( P )</td>
<td>&lt; 0.001 - 0.617</td>
<td>&lt; 0.001 - 0.460</td>
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**DISCUSSION**

We detected dependence among individuals in all 3 herds of bighorn sheep using nearest-neighbor analyses. It is inappropriate to consider data for each ewe as an independent sample of movement or habitat use. Instead of 15 independent samples of individual use, we have 3 independent samples of herd use.

Before pooling these data, we considered the difference between statistical dependence and biological dependence. Millspaugh et al. (1998) insisted the researcher consider the biology behind dependence before deciding how to treat data. We present examples used in their discussion. African hunting dogs (*Lycaon pictus*) are obligatory cooperative hunters, so 5 radio-collared hunting dogs would move and hunt as 1 pack. The appropriate sample is the pack, and data from individuals should be pooled. Now consider a group of 5 radio-collared elk (*Cervus elaphus*) that converge on a patch of winter range. Though they are together on the same habitat all winter, it is conceivable that each elk made an independent choice to be there when suitable winter range is
scarce. In this case, statistics may show a lack of independence, but biologically, one might still consider each elk an independent sample (Millspaugh et al. 1998).

In the case of bighorn sheep, one might argue that ewes congregate on steep, cliffy habitat during lambing season because it is the best habitat, not because of dependency. Perhaps each ewe makes an independent choice to be there. However, grouping behavior and social dependency are consistent, year-round characteristics of bighorn sheep (Geist 1971). This suggests they are both statistically and biologically dependent.

We do not, however, believe that bighorn data from a given site should always be pooled due to lack of independence. Festa-Bianchet (1986) found that a single area was used by 3 distinct populations of bighorn ewes during different times of the year. A test of spatial independence with such data would reveal independence between groups, and prevent the loss of information by pooling across independent study animals.

Limited solutions are available when a lack of independence has been detected in a set of data. In terms of resource selection, we consider 2 ways of defining the sample unit. In analyses where the relocation is the sample unit (Neu et al. 1974, Manly et al. 1993), we suggest data be pooled, switching the sample unit from the locations of individuals to the location of groups. In this way, a group of 5 radio-collared animals in the same place would be recorded as a single location, and a single radio-collared animal in a different place would be another group location (a group of 1). Different weights might be placed on these types of data for future resource selection analysis.

In analyses where the animal is the sample unit (Johnson 1980, Aebischer et al. 1993), a solution is less evident. If there are multiple social groups of dependent animals,
(but the groups remain independent), then the sample unit might become the social group. This could require much data, as in the case of our 3 herds of bighorn sheep; we have 3 independent populations, and n is only 3.

Dasgupta and Alldredge (2000) adjusted the Neu et al. (1974) method of analysis to incorporate dependency. Their dependency parameter over-simplifies the spatial and temporal nature of simultaneous telemetry data, but this is a promising approach to analysis. They include the degree of independence as an additional parameter in resource selection analysis. Unfortunately, such a technique is not available for more sophisticated analyses like compositional analysis or generalized linear modeling.

While we have focused on \textit{a posteriori} detection and solutions to spatial independence, this is an issue that should be considered \textit{a priori} in future studies. Before expending great effort and resources into marking dependent animals, we encourage researchers to consider the biology and behavior of the study species. A preliminary look at the species of interest might reveal social groups across which collars or marks should be spread. Spatial independence is an important assumption in the study of resource selection by animals. Both \textit{a priori} and \textit{a posteriori} consideration of this issue in combination with the biology and behavior of the species of concern will improve the reliability of results.

\textbf{LITERATURE CITED}


Chapter 3. Bighorn Sheep, Horizontal Visibility, and GIS

Abstract: Habitat evaluation procedures are commonly used in bighorn sheep (*Ovis canadensis*) reintroduction and restoration, and many of these models incorporate high horizontal visibility as necessary for suitable bighorn habitat. Other variables like cover type and canopy closure are easier to quantify and often are used as indices for horizontal visibility. Few studies have directly measured bighorn sheep preferences of horizontal visibility without using such indices. We measured horizontal visibility at a sample of locations used by sheep and paired locations 200 m away at 3 sites in western Montana, and we did not detect significant differences. We also used multiple regression and analysis of variance to assess the relationship between horizontal visibility and 3 explanatory variables easily quantified in a GIS (cover type, slope, and aspect). All 3 of our explanatory variables had significant relationships with horizontal visibility (*P* ≤ 0.001). Simple indices such as cover type alone are insufficient to accurately predict horizontal visibility.

INTRODUCTION

Bighorn sheep suffered a dramatic population decline and reduction in geographic range during the latter part of the 19th century. Intensive restoration and translocation efforts begun during the 1950’s have since returned their numbers from an estimated 20,000 in the contiguous U.S. in 1960 to nearly 50,000 in 1991 (Buechner 1960, Valdez and Krausman 1999). Sheep were extirpated from much of their native range, so these restoration efforts have focused on returning populations to unoccupied but suitable habitat. Bighorns rarely recolonize areas through dispersal due to strong site fidelity.
(Geist 1970, 1971), so management has been focused on artificial translocations and reintroductions (Hansen et al. 1980).


One such habitat feature, horizontal visibility (estimated as a percentage from 0-100), relates to the preference of bighorn sheep for open areas with little visual obstruction. Their predator avoidance strategy relies on an ability to detect danger at a distance, giving them ample time to retreat to safer terrain when needed (Geist 1971, Risenhoover and Bailey 1980).

We found few studies that directly measured bighorn sheep preference of horizontal visibility. Hayes et al. (1994) measured visibility at 70 locations used by a captive population of bighorn sheep, and compared these to measures of visibility at 30 randomly selected points within the same area. They did not find a significant difference in visibility between used and random sites. McCarty (1993) also sampled used and random points within a study area for visibility, and he did detect preference of more open areas. Etchberger et al. (1989) found significantly higher visibility values in areas used by sheep than those in a neighboring unused area.
Risenhoover and Bailey (1985) found habitat types preferred by sheep provided greater visibility than avoided habitat types. Their study was the more typical approach to horizontal visibility: this involved associating it with another habitat variable such as cover type or canopy closure. For example, field measures are used to estimate an average visibility for each cover type in a study area. Preference or avoidance of a cover type is then inferred to indicate preference or avoidance of the associated level of horizontal visibility. In this way, the biologists are not truly measuring the animal’s preference for horizontal visibility, but are instead attributing different levels of preference between cover types to visibility. This is an indirect and potentially confounded assessment of how bighorn sheep respond to horizontal visibility.

Accurate measures of horizontal visibility come from site-specific work in the field, but indices are often used to incorporate this variable into habitat modeling (Hansen 1980, Holl 1982, Smith et al. 1991, Johnson and Swift 2000). This is also done by associating levels of visibility with different cover types or levels of canopy closure. Recently, the use of geographic information systems (GIS) and satellite imagery data has become popular in habitat modeling. However, horizontal visibility is a variable that escapes direct measurement through remotely-sensed data.

In this paper, we address 2 key questions concerning horizontal visibility and habitat modeling with regards to bighorn sheep habitat selection. First, we directly estimated the relationship between bighorn sheep habitat use and horizontal visibility by measuring visibility in the field at sites used by wild bighorn sheep and paired “available” sites. This avoided the problem of using selection of cover types to infer selection of horizontal visibility. However, we acknowledge that some index of horizontal visibility
is required for future modeling in the GIS environment. Our second objective was to test what other habitat variables, if any, could be used to accurately predict horizontal visibility in a GIS framework.

**METHODS**

**Do bighorn sheep prefer sites with higher horizontal visibility?**

We captured 21 bighorn sheep among 3 herds in western Montana in March, 2001, using net-gunning from a helicopter (Krausman et al. 1985). We used radiotelemetry between March, 2001 and August, 2002, to collect locations of groups of radio-collared sheep among these 3 herds (Bearmouth, Garrison, and Skalkaho). We selected a systematic sample (every other location) of these locations for field measurements of horizontal visibility. For each of these selected “use” locations, we selected another location 200 m away in a random direction to measure visibility at “available” sites. To avoid disturbing sheep, we did not measure visibility at these sites on the same day in which sheep were located. The time period between locating sheep and returning to measure visibility ranged between 1 week and 12 months, which meant vegetative conditions during measurement were not always the same as when sheep were observed. We always measured visibility for both the use and the available sites during the same day, so we believe a valid estimate of the relative difference between them was maintained.

We used the staff-ball method to estimate horizontal visibility in the field (Collins and Becker 2001). Collins and Becker (2001) found this method to be more precise than both the cover-pole (Griffith and Youtie 1988) and checkerboard target (Nudds 1977,
Smith and Flinders 1991), and we found it convenient in the field because it required only a single person. We cut 2 holes through a bright orange tennis-ball and mounted it on top of a gardening stake (staff); the staff was driven into the ground at the location of interest, and the bottom of the tennis ball was adjusted to 90 cm above the ground (Risenhoover and Bailey 1985). The observer walked a circle around the staff with a radius of roughly 20 m. While walking this circle, the observer stopped every eighth step and, with his or her eye-level also at 90 cm, looked for the “dimensionless point” where the ball and the right side of the staff intersected (Collins and Becker 2001). Collins and Becker (2001) suggested using the point of intersection between the ball and staff to yield a distinct yes or no result instead of subjective estimates or counts used with other methods. After completing the circle, the observer divided the number of times the point was visible by the total number of attempts, e.g. 12 visible/20 total = 60% horizontal visibility.

A biologically meaningful radius to measure visibility was difficult to select. A radius of 20 m was used in previous studies of horizontal visibility (McCarty and Bailey 1992) and fell in between other commonly used distances of 14 m (Risenhoover and Bailey 1980, Smith and Flinders 1991), 28 m (Johnson and Swift 2000) and 40 m (Risenhoover and Bailey 1985, Hayes et al. 1994). Twenty meters also corresponded to the diagonal radius of a 30 m by 30 m pixel which is the spatial scale of our GIS data.

We used a paired-samples T-test to detect differences between horizontal visibility at used and available sites. We analyzed data separately for each sex at each of 3 study sites (Bearmouth, Garrison, and Skalkaho). Bighorn sheep are known to have seasonal ranges, and make different tradeoffs in habitat selection to accommodate seasonal needs. For example, ewes may sacrifice forage quality for lamb security by
retreating to rocky outcroppings in the spring. We suspected that horizontal visibility might have varied importance throughout the year so we divided ewe locations into 3 biologically meaningful seasons (winter, lambing, fall) for each herd and analyzed seasons separately. Roughly, the lambing season lasted from early May through late July, the fall season from early August through late November, and the winter season from early December through late April. The number of ram locations was insufficient to separate by season.

**Can we model horizontal visibility in a GIS?**

We did a simple exercise in modeling horizontal visibility using several predictor variables. We compiled GIS data sets for each of the 3 study sites (Bearmouth, Garrison, and Skalkaho). We began with 2 vegetation layers commonly associated with horizontal visibility, cover type and canopy cover, with 30 m x 30 m resolution (Wildlife Spatial Analysis Lab, The University of Montana 2001). We reduced our cover type layer into 3 categories: xeric grass/shrub lands (Grass), open forests (OpenFor), and closed forests (ClosedFor). Two of the 3 study sites were burned during the fires of 2000, which was after the vegetation layers were created. We used fire severity GIS layers to add 3 more categories to our cover type layer: burned grass/shrub (GrasBurn), low-moderately burned forest (LowBFor), and severely burned forest (SevBFor) (Wildlife Spatial Analysis Lab, The University of Montana 2000). We were unable to correct the canopy cover layer for changes due to the fires, so the canopy cover data were omitted from the modeling process.
While vegetation certainly affects horizontal visibility, our field measurements were just as often affected by the topography of the area. Ridges and valleys often concealed the staff-ball target, even when the vegetation was open grassland. For this reason, we suspected that topographic variables like slope, aspect, or ruggedness might also contribute to some of the variation in horizontal visibility. Terrain ruggedness is often quantified by the density of contour lines on area maps (Beasom et al. 1983), and Ebert (1993) found it was highly correlated with slope values. Because of this correlation between ruggedness and slope, we used only slope and aspect layers created from the USGS National Elevation Data Set DEM, with a pixel size of 30 m x 30 m. We left slope as a continuous variable and categorized aspect into 1 of the 4 cardinal directions (N, S, E, W).

We pooled the use and availability locations for this analysis, and associated each location with a value for cover type, slope, and aspect from the GIS. To avoid sampling bias between sites, we randomly selected 100 points from each site for analysis. Before modeling, we visually assessed the relationships between predictor variables and horizontal visibility using simple boxplots and scatterplots. We then used multiple regression and analysis of variance to assess the relationship between each predictor variable and horizontal visibility. We began with a saturated model (all 3 predictor variables) and used the Type III Extra-Sums-of-Squares F test to assess variable significance. We used Student’s T tests to evaluate parameter coefficients.

RESULTS

Do bighorn sheep prefer sites with higher horizontal visibility?
Visibility did not appear to be a significant variable at this scale of habitat selection ($P = 0.013 - 0.968$). We measured visibility at 644 locations (322 used, 322 available, Table 1). None of the tests for ewes at any site or season gave results indicating significant differences in visibility between used and available locations. When ewe data were pooled across seasons, results remained insignificant. Effect sizes were very small, but the magnitude of the difference did indicate generally higher visibility values at used sites during winter and fall. Ram data were pooled across all seasons, and 2 of the 3 sites revealed significantly higher visibility for used sites.

**Table 1.** Paired-samples T-tests compare horizontal visibility values for paired used and available locations for bighorn sheep at 3 study sites, 2001-2002. Means of used/available values, the sample size of paired values, and $P$-values are presented.

<table>
<thead>
<tr>
<th>Site</th>
<th>Sex</th>
<th>Season</th>
<th>Bearmouth used/avail</th>
<th>Garrison used/avail</th>
<th>Skalkaho used/avail</th>
<th>P-used/avail</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ewe</td>
<td>Winter</td>
<td>56/51 n=24</td>
<td>68/64 n=39</td>
<td>66/63 n=45</td>
<td>0.364</td>
<td>0.289</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lambing</td>
<td>53/54 n=13</td>
<td>48/44 n=38</td>
<td>56/60 n=29</td>
<td>0.913</td>
<td>0.437</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fall</td>
<td>62/49 n=9</td>
<td>60/71 n=28</td>
<td>58/53 n=30</td>
<td>0.204</td>
<td>0.105</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pooled</td>
<td>56/51 n=46</td>
<td>59/59 n=105</td>
<td>61/59 n=104</td>
<td>0.279</td>
<td>0.968</td>
</tr>
<tr>
<td></td>
<td>Ram</td>
<td>Pooled</td>
<td>69/49 n=25</td>
<td>67/67 n=31</td>
<td>65/52 n=39</td>
<td>0.028</td>
<td>0.935</td>
</tr>
</tbody>
</table>

Can we model horizontal visibility in a GIS?
Simple boxplots and scatterplots did reveal some visual relationships between predictor variables and horizontal visibility. For example, changes in cover type had apparent effects on visibility values (Figure 1).

**Figure 1.** Box plots of horizontal visibility values for each category of cover type at 3 study sites in western Montana, 2001-2002.

The Type III Extra-Sums-of-Squares F test revealed significant relationships between horizontal visibility and all 3 predictor variables: slope \( (P = 0.001) \), cover type \( (P < 0.001) \) and aspect \( (P < 0.001) \). Slope and visibility were negatively correlated, so higher slopes led to lower visibility (Table 2). Cover type and aspect are categorical variables, so coefficients presented in Table 2 are relative to an alias or reference category; grassland was the alias category for cover type and South the alias category for Aspect. All categories of cover type had lower values of horizontal visibility than grasslands, and West and North aspects had higher values of horizontal visibility than South aspects.
Table 2. Parameter estimates for multiple regression modeling of horizontal visibility data in bighorn sheep habitat in western Montana, 2001-2002. Coefficients and $P$-values for categories of Cover Type and Aspect are relative to their respective alias categories.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\beta$</th>
<th>Std. Error of $\beta$</th>
<th>t</th>
<th>$P$</th>
<th>95% Confidence Interval for $\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>80.927</td>
<td>4.584</td>
<td>17.655</td>
<td>0.000</td>
<td>(71.905, 89.948)</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.530</td>
<td>0.164</td>
<td>-3.226</td>
<td>0.001</td>
<td>(-0.853, -0.207)</td>
</tr>
<tr>
<td>OpenFor</td>
<td>-14.984</td>
<td>6.171</td>
<td>-2.428</td>
<td>0.016</td>
<td>(-27.129, -2.840)</td>
</tr>
<tr>
<td>ClosedFor</td>
<td>-29.612</td>
<td>4.225</td>
<td>-7.009</td>
<td>0.000</td>
<td>(-37.927, -21.297)</td>
</tr>
<tr>
<td>LowBFor</td>
<td>-23.752</td>
<td>6.192</td>
<td>-3.836</td>
<td>0.000</td>
<td>(-35.939, -11.565)</td>
</tr>
<tr>
<td>SevBFor</td>
<td>-14.662</td>
<td>4.900</td>
<td>-2.992</td>
<td>0.003</td>
<td>(-24.306, -5.018)</td>
</tr>
<tr>
<td>West</td>
<td>12.838</td>
<td>3.667</td>
<td>3.501</td>
<td>0.001</td>
<td>(5.620, 20.055)</td>
</tr>
<tr>
<td>North</td>
<td>4.928</td>
<td>5.090</td>
<td>0.968</td>
<td>0.334</td>
<td>(-5.090, 14.947)</td>
</tr>
<tr>
<td>East</td>
<td>-1.970</td>
<td>3.751</td>
<td>-0.525</td>
<td>0.600</td>
<td>(-9.352, 5.413)</td>
</tr>
</tbody>
</table>

a Alias variable for Cover Type = Grassland
b Alias variable for Aspect = South

**DISCUSSION**

We detected significant preference for areas of high visibility in the rams of 2 of our 3 study sites; it is questionable whether the magnitude of these differences (mean differences in % visibility of 20 and 10) are biologically significant. Selection was not observed for ewes for any season or site, though the magnitude of the differences
indicated generally higher visibility at used sites during fall and winter. A biological explanation might suggest that ewes protecting lambs sacrifice good forage and high visibility for other habitat features like steep slopes and escape terrain, where rams, unhindered by young, choose areas with better forage and high visibility. However, the scale of our analysis could also explain the results.

We used a radius of 20 m to measure visibility, which is an important decision of scale. Sheep may perceive horizontal visibility at smaller or larger scales than this 20 m radius. Measurement at another radius might yield different results. Our comparisons were also limited to used sites and paired available sites 200 m away. This 200 m distance might not be adequate to detect habitat preferences. Perhaps the sheep are making selections at much larger scales, so the observer would have to go further than 200 m to get an appropriate comparison.

Risenhoover and Bailey (1985) found that visibility was an important habitat characteristic until a threshold was reached, beyond which other variables became more important. In terms of Johnson’s (1980) different scales of selection, visibility might be an important variable of second order, or home range, selection. Third order selection occurs within the home range. For a bighorn sheep, much of this area might already exceed some threshold of horizontal visibility, and other fine-scale variables become more important. Because our methods were really measuring third-order selection (within the home range), we would be unable to detect any selection going on at a larger scale.

The average visibility values for sites used by ewes in each herd (56%, 59%, 61%) were all considerably lower than that required by Smith et al.’s (1991) bighorn
habitat suitability model. Their model designated all areas with visibility less than 80% as unsuitable for bighorn sheep. Cut-offs of 62% (Johnson and Swift 2000) or 55% (Zeigenfuss et al. 2000) seem more reasonable given our data, and researchers and managers might be more liberal with this parameter in future bighorn habitat modeling. The lag-time between observed use of a site and the follow-up measurement of visibility in our data may bias our mean visibility values.

Several variables were correlated with horizontal visibility. Though our intent was to use all reasonable predictor variables in modeling, much unexplained variation remained. Our vegetation data were simplified into a few basic classes. More detailed and accurate distinctions between vegetation types may be possible as the quality of these remotely sensed data improves. Topography appeared to have important relationships with visibility, and more complex measures of topographic diversity might be incorporated into future modeling. Landscape configuration measures such as the diversity of aspects or slopes within a given radius might better estimate subtle topographic barriers to visibility. Divine et al. (2000) found that the resolution of digital elevation model (DEM) data had a significant effect on measures of terrain ruggedness. Thirty meter pixel sizes provided more precise measures of topographic variables such as slope than 100 m pixels. Future development of 10 m resolution DEM data in some areas may further improve our ability to quantify topography for visibility estimation.

We recommend researchers take into account the highly variable nature of horizontal visibility values before using simple indices like cover type to quantify it. Multiple regression modeling procedures such as ours may be useful in certain, site-specific cases to accurately predict horizontal visibility in a GIS framework.
LITERATURE CITED


investigations and management recommendations. Utah Division of Wildlife Resources, research final report. 425 pp.


Chapter 4. Evaluation of resource selection models with naturally recolonized bighorn sheep habitat

Abstract: Habitat suitability models are an important tool in bighorn sheep (Ovis canadensis) restoration and reintroduction efforts, but few of these models have been developed in areas naturally recolonized by sheep. We used logistic regression and resource selection function (RSF) methods to generate RSF models for 3 naturally recolonized bighorn sheep habitats in western Montana. Increasing slopes and decreasing distances to escape terrain were important in most models, but relationships were inconsistent for other explanatory variables. Initial evaluation of models using data from the site where they were created revealed excellent fit and predictive accuracy ($P < 0.002$). However, testing models across sites with independent testing data gave mixed results, and in many cases poor fit ($P = 0.001 - 0.960$). Site-specific variation accounted for mixed results in fitting models across sites, and we encourage caution when drawing conclusions from resource selection analyses of local data.

INTRODUCTION

Bighorn sheep suffered a dramatic population decline and reduction in distribution during the latter part of the 19th century. Restoration efforts begun in the 1950’s have focused on translocations and reintroductions into habitat deemed suitable but unoccupied (Hansen et al. 1980). To maximize the success of continued translocation efforts, much emphasis has been placed on identifying suitable bighorn habitat through

Due to their current existence in fragmented populations and the insular nature of their habitat (Hansen 1980), sheep were thought to be poor dispersers with very strong site fidelity (Geist 1970, 1971). However, metapopulation dynamics can exist among subpopulations of sheep (Schwartz et al. 1986; Bleich et al. 1990, 1996), and bighorn sheep do have the capacity to naturally recolonize habitats (Singer et al. 2000). In these cases, sheep are making their own decisions about habitat suitability. An attractive research aim would be to develop habitat suitability models based on these naturally colonized areas. In other words, “What habitat do dispersing sheep deem suitable?” However, with so much site-specific variation possible, it is unclear if habitat features selected by dispersing sheep are consistent.

Three herds of bighorn sheep have naturally recolonized previously unoccupied habitat in western Montana within the past 20 years. Though these recolonizations are partially the result of transplanting sheep into other nearby source populations, they remain as newly established herds in habitats chosen independently by dispersing sheep. We used resource selection function (RSF) methods (Manly et al. 1993, Boyce et al.
to study and compare the habitat selection of these 3 herds. Our data focus on
Johnson’s (1980) third-order selection, or selection of habitat within the home range. We
developed and evaluated RSF models for each herd. We then applied a more rigorous
test of each model by using testing data from the other 2 sites to examine the dangers of
applying site-specific models across larger landscapes (Verbyla and Litvaitis 1989,
Fielding and Bell 1997, Boyce et al. 2002). Such a comparison also tests whether
recolonized populations select resources similarly.

METHODS

Study Area

We studied the resource selection of bighorn sheep in 3 recolonized areas
(Bearmouth, Garrison, and Skalkaho) in western Montana. Each site is roughly 70 km
from the other 2 sites, and other well established bighorn herds exist in between. All 3
herds occupy low-mid elevation habitats where common native grassland species are
bluebunch wheatgrass (Agropyron spicatum), Idaho fescue (Festuca idahoensis), and
rough fescue (Festuca scabrella); shrub species include sagebush (Artemesia tridentata)
and mountain mahogany (Cercocarpus ledifolius); and forests are dominated by open
stands of ponderosa pine (Pinus ponderosa) and denser stands of Douglas-fir
(Pseudotsuga menziesii). Exotic species such as cheatgrass (Bromus tectorum) and
spotted knapweed (Centaurea maculosa) are also common.

Data Collection and Pooling

In March, 2001, we captured and radio-collared 16 adult female bighorn sheep at
3 sites using a net-gun from a helicopter (Krausman et al. 1985). We attempted to
capture animals from different subgroups within each herd, and ended with 2
(Bearmouth), 7 (Garrison) and 7 (Skalkaho) radio-collared animals per site. Small
numbers of rams captured (n=2, 2, 1, respectively) prevented their inclusion in this
analysis. Between March, 2001 and August, 2002 we used radio-telemetry primarily
from the ground to collect 1,034 locations for collared ewes.

We maintained a minimum of 3 days between relocating sheep to ensure temporal
independence in the data (Swihart and Slade 1985, McNay et al. 1994, Otis and White
1999). Swihart and Slade (1985) suggested that the time to independence (TTI) should
be the amount of time for the animal to traverse its entire home range. This allows the
animal to make a new habitat choice, independent of the last. Following Swihart et al.’s
(1988) measure of TTI for successive relocations, Ebert (1993) determined a minimum of
15.9 hours as the time interval necessary to eliminate autocorrelation between
observations of the bighorn sheep in his study; this estimate is far below our minimum.

Based on our movement data and observations, 3 days seemed more than enough time to
ensure independent locations for bighorn sheep.

We used a modified nearest-neighbor analysis to test for spatial independence
between individual ewes within a herd (Chapter 2, this thesis). The movements of each
collared ewe in a herd were highly dependent on those of other collared ewes. This
suggested a lack of independence in relocations among individuals, which can bias
habitat selection results (Millspaugh et al. 1998, Dasgupta and Alldredge 2000), so we
pooled data within each herd. Our sampling unit became the location of a group of
sheep, which may have included a single or multiple collared animals. This reduced our
sample size from 1,034 individual locations to 523 group locations.
Bighorn sheep are known to select resources differently according to season. We divided data for each herd into 3 biologically meaningful seasons (winter, lambing, and fall). We used shifts in movements or behavior to delineate locations of each individual into each season. For example, ewes often exhibit a clear movement to an isolated area of rugged terrain when they are preparing to lamb. We observed these shifts, but noted that they did not occur on the same date for each ewe. Thus, we considered the categorization of locations into seasons on an individual by individual basis. Roughly, the lambing season lasted from early May through late July, the fall season from early August through late November, and the winter season from early December through late April. Separating data by study site resulted in 3 separate models for each of these 3 seasons. We pooled data for the same season across years based on a subjective assessment of similar movements. Sample sizes of group locations per site and season are presented in Table 1.

**Table 1.** Sample sizes of bighorn ewe group locations for each site and season, 2001-2002.

<table>
<thead>
<tr>
<th>Season</th>
<th>Bearmouth</th>
<th>Garrison</th>
<th>Skalkaho</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>47</td>
<td>69</td>
<td>95</td>
</tr>
<tr>
<td>Lambing</td>
<td>49</td>
<td>72</td>
<td>76</td>
</tr>
<tr>
<td>Fall</td>
<td>20</td>
<td>51</td>
<td>44</td>
</tr>
</tbody>
</table>

**Habitat Variables**

We reviewed the habitat selection and modeling literature for bighorn sheep to select appropriate explanatory variables for RSF modeling (Table 2). We compiled these data in a GIS using ArcView 3.2a and the Spatial Analyst extension. We derived 30 by 30 m grids of elevation, slope, and aspect (divided into 3 indicator variables based on the
4 cardinal directions) from the USGS National Elevation Dataset. We also derived a solar radiation index (SRI) combining latitude, slope, and aspect that has proven a significant predictor of bighorn sheep habitat use (Dicus 2002; K. Keating, USGS, personal communication). This SRI is an index of the amount of solar radiation received by a given area, and may correlate to bighorn habitat use based on their frequent use of steep, south-facing habitats. We defined areas with slopes > 27° as escape terrain (Smith et al. 1991, McCarty 1993, Dunn 1996, Andrew et al. 1999), and quantified the distance from escape terrain patches. We created a minimum patch size for escape terrain (0.713ha) based on the smallest patch that we observed sheep using for escape. We edited TIGER 2000 Census data to measure distance to water and distance to roads.

**Table 2.** Descriptions of variables derived from GIS to quantify resource selection of bighorn sheep, western Montana, 2001-2002. All data had pixel resolution of 30 m x 30 m.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>ELEV</td>
<td>Elevation (m)</td>
</tr>
<tr>
<td>SLOPE</td>
<td>Slope (deg)</td>
</tr>
<tr>
<td>ASPN</td>
<td>North aspect (indicator variable)</td>
</tr>
<tr>
<td>ASPE</td>
<td>East aspect (indicator variable)</td>
</tr>
<tr>
<td>ASPW</td>
<td>West aspect (indicator variable)</td>
</tr>
<tr>
<td>SRI</td>
<td>Solar radiation index</td>
</tr>
<tr>
<td>DISESCP</td>
<td>Distance to nearest escape terrain (m)</td>
</tr>
<tr>
<td>DISWATR</td>
<td>Distance to nearest water (m)</td>
</tr>
<tr>
<td>DISROAD</td>
<td>Distance to nearest road (m)</td>
</tr>
<tr>
<td>DISGRAS</td>
<td>Distance to nearest xeric grass/shrubland (m)</td>
</tr>
<tr>
<td>DISOPFOR</td>
<td>Distance to nearest open canopy forest (m)</td>
</tr>
<tr>
<td>DISCLFOR</td>
<td>Distance to nearest closed canopy forest (m)</td>
</tr>
<tr>
<td>DISBGRA</td>
<td>Distance to nearest burned grasslands, burned summer 2000</td>
</tr>
<tr>
<td>DISLBFOR</td>
<td>Distance to nearest low-severity burned forest, burned summer 2000</td>
</tr>
<tr>
<td>DISHBFOR</td>
<td>Distance to nearest high-severity burned forest, burned summer 2000</td>
</tr>
</tbody>
</table>

We used the SILC3 Land Cover Classification Data (Wildlife Spatial Analysis Lab, The University of Montana 2001) to quantify vegetation types at 30 m x 30 m.
resolution. These data consisted of many cover types which we simplified into 3 basic categories of cover type (xeric shrub and grassland, open canopy forest, and closed canopy forest). Rare and poorly delineated cover types such as riparian areas were not included to avoid spurious results. Two of the 3 study sites experienced wildfires during the summer of 2000, after the SILC3 data were created. We used fire severity data from (Wildlife Spatial Analysis Lab, The University of Montana 2000) to edit the SILC3 vegetation data and create 3 additional vegetation classes (burned grass, low-severity burned forest, and high-severity burned forest). High-severity burned forests were typically open areas with bare snags and fresh grass and forb regrowth. Low-severity burned forests retained more needles and tree canopy, leaving them denser than high-severity areas. We included these cover types in habitat selection models as 6 separate variables by quantifying the distances from locations to each cover type (Miller et al. 2000). Miller et al. (2000) discussed the logic of using distances to habitats. It is likely that animals select habitat on many scales, so the configuration of different habitats around them may be as important as the single habitat they are in at a given moment. Measuring distance to each cover type is one rough measure of this configuration.

Many bighorn habitat studies or habitat suitability models have highlighted horizontal visibility as a key component of bighorn habitat (Risenhoover and Bailey, 1980, 1985; Smith et al. 1991; Johnson and Swift 2000; Zeigenfuss et al. 2000). We did not find strong preferences for areas with high horizontal visibility (Chapter 3, this thesis). In addition, data commonly used to index horizontal visibility such as cover type layers in a GIS were not found to be adequate predictors of horizontal visibility in the
field (Chapter 3, this thesis). For these reasons we did not include horizontal visibility as an explanatory variable in our modeling.

**Data Analysis**

The core of our analysis is comparing habitat used by animals to the habitat available to them. Locations of groups of bighorn sheep ewes provide a sample of used habitat. Definitions of available habitat are somewhat arbitrary (Aebischer et al. 1993, Wilson et al. 1998); we used a 100% minimum convex polygon (MCP) with an additional buffer of 100 m as the herd home range to best approximate the area available during the study period (McCorquodale 1999). Seasonal home ranges overlapped greatly, and sheep are probably familiar with all parts of their annual home range. We used a single year-round home range to define available habitat at each site. A very small subset of locations (n=3) gathered during migrations to outlying areas not considered part of the home range (Burt 1943) were removed before calculating MCPs.

We drew a systematic sample points from a 100m x 100m grid within MCPs to generate a large sample of habitat availability locations (Erickson et al. 1998).

We used logistic regression to calculate a resource selection function for each site and season (Manly et al. 1993). Logistic regression is based on a binary response variable, coding used locations as 1’s and available locations as 0’s. Using logistic regression to create an RSF from use/availability data presumes that the probability of sampling a used location from the population of all used locations is known (Manly et al. 1993). This probability is part of estimating the constant ($\beta_0$) in the logistic equation. With radio-telemetry data alone, it is not possible to estimate this probability because we cannot quantify the population of used locations. A resource selection function can still
be estimated using standard logistic regression procedures, but before applying it to make predictions, the constant term ($\beta_0$) is removed. This leaves the RSF as simply the explanatory parameters and their coefficients. Though not scaled between 0 and 1, the resulting predicted values still provide an index of the probability of use (Manly et al. 1993, Campos et al. 1997).

**Model Selection**

Adhering to the information-theoretic approach to model selection (Burnham and Anderson 1998), we developed a set of 10 *a priori* candidate models for each season based on literature review and observation of seasonal habitat preferences of bighorn sheep. For example, when creating candidate models for the lambing season, we focused on slope and distance to escape terrain to account for the importance of safe, rugged lambing terrain. The literature is inconsistent on the importance of nearby water for lambing habitat, so we created models that both included and excluded this variable. We treated the distance to cover type variables as a set of parameters for inclusion in candidate models. When this set of cover type variables was included, we removed categories that did not seem biologically relevant (e.g. we excluded the 3 classes of burned cover types from modeling at the Garrison site, because no fires occurred nearby).

Before proceeding with model selection, we fit global models with all meaningful explanatory variables and used the Hosmer and Lemeshow goodness-of-fit test to ensure general model fit (Burnham and Anderson 1998, Hosmer and Lemeshow 2000). A poor-fitting global model would suggest the fit of candidate models will be poor.

We used the same set of seasonal candidate models for each site (with some variation in the included cover type categories), and calculated $AIC_c$ values to
discriminate the fit and parsimony of candidate models. Akaike Information Criteria are biased towards models with many parameters as sample size increases (Hastie et al. 2001). We found this problematic because our large systematic samples of availability (n = 2,428, 1,204, 1,953 for the 3 study sites) led to the consistent selection of the most complex models. To compensate, we randomly selected 200 locations from the systematic samples to quantify availability and found that AIC$_c$ selected more parsimonious models. We calculated the differences in AIC$_c$ values from the lowest scoring model ($\Delta_i$) and Akaike weights ($w_i$) for each candidate model. When multiple models score $\Delta_i$ values < 2, the single, best model is unclear (Burnham and Anderson 1998). We found that model averaging procedures based on Akaike weights resulted in parameter-heavy, complex models. When multiple models scored $\Delta_i < 2$, we selected the model with the fewest parameters as the best model to maintain parsimony. We re-ran that best model with the full systematic sample of availability locations to obtain more precise coefficient estimates that remain unbiased (Burnham and Anderson 1998; T. McDonald, West, Inc., personal communication).

**Model Evaluation**

Careful evaluation of wildlife habitat models is an important step in maintaining their value for conservation. A practical test of these models is less concerned with statistical fit, and more concerned with their ability to make reliable predictions about habitat use (Boyce et al. 2002). Testing model predictions using the same data that were used to create the model can lead to optimistically biased estimates of model accuracy (Verbyla and Litvaitis 1989, Chatfield 1995, Fielding and Bell 1997). We used this method to check the initial fit of our models to their respective datasets. A model
selection approach with small sets of parsimonious candidate models serves to minimize
the dangers of overfit and optimistically biased evaluations.

When there is only one data set available to create and evaluate the models,
resampling methods like bootstrap or jackknife procedures can be used to increase
precision. However, Chatfield (1995) warned that these methods can increase precision
without necessarily eliminating bias. The rare, but ideal, situation is when a second,
independent data set is available for model testing. Our samples of 3 independent herds
provided such an opportunity. We applied models across sites for an unbiased test of
model performance in the face of independent test data. Testing models across sites also
measures how similarly ewes of different herds select habitat.

We used a method proposed by Boyce et al. (2002) to evaluate the prediction
success of our models. This method calculates the degree of correlation between
predicted probabilities and measured use. When a model is applied to a site in GIS, each
pixel is assigned a prediction score. This test compares the distribution of model
predictions to the set of locations actually used by sheep within the site. We used SPSS
to divide the range of model prediction scores into 10 similar-sized sample bins from
lowest to highest scoring. The 10 bins create 10 zones of space with increasing
probabilities of use by sheep. We calculated the density of sheep locations within each
bin by dividing the number of sheep locations in a bin, by the area of that bin across the
landscape. Thus, a bin with a high number of locations in a small area received a high
score; or a bin that comprised much area but few locations received a low score. We
used a Spearman-rank correlation to see how well the density scores for each bin
correlated with that bin’s ranking in prediction score (Boyce et al. 2002). If the bins with
the highest probability predictions also have the highest density of sheep locations, and vice-versa, the Spearman-rank correlation returns significant results. We also used scatterplots to visually assess these relationships.

RESULTS

We found both similarities and differences in best models across seasons and sites (Table 3, Appendix A). Increasing slopes and decreasing distances to escape terrain appeared to be important explanatory variables in most cases. While distance to water was a significant explanatory variable in 2 of the 3 lambing models, the sign of the coefficient revealed that ewes during the lambing period were actually further from water than expected. The solar radiation index (SRI) proved a valuable explanatory variable in several cases, while aspect was not in a single “best” model.

Models performed extremely well when applied at the site where they were created (Table 4). This gives us confidence that selected models are reliable estimates of habitat selection for given sites and seasons. Comparing models across sites revealed many differences.
Table 3. Variables and coefficient signs included in season and site-specific best models for bighorn sheep resource selection at 3 sites in western Montana, 2001-2002. Habitat variables are described in Table 2, and coefficients and standard errors are presented in Appendix A.

<table>
<thead>
<tr>
<th>Season</th>
<th>Site</th>
<th>ELEV</th>
<th>SLOPE</th>
<th>SRI</th>
<th>DISESCP</th>
<th>DISWATR</th>
<th>DISROAD</th>
<th>DISGRAS</th>
<th>DISOPFOR</th>
<th>DISCLFOR</th>
<th>DISBGRAS</th>
<th>DISLBFOR</th>
<th>DISHBFOR</th>
</tr>
</thead>
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<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Skalkaho</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+</td>
<td></td>
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<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>+</td>
<td>-</td>
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<td></td>
<td></td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Skalkaho</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>Garrison</td>
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<td>+</td>
<td></td>
<td></td>
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<td>Skalkaho</td>
<td>+</td>
<td>-</td>
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<td></td>
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<td></td>
<td>+</td>
<td>-</td>
<td>+</td>
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</tr>
</tbody>
</table>

Bearm  ooth = Bearmouth
The same candidate models (with differences in included cover type categories) were used to select a “best” model for each site. Only in the winter models for Bearmouth and Skalkaho were the same candidate models (with different coefficients) chosen; different candidate models were selected for different sites in all other cases.

Table 4. Spearman rank-correlations and associated $P$-values testing correlation between season and site-specific resource selection model predictions and relocation data for bighorn sheep at 3 sites, 2001-2001. Values in bold represent unbiased tests of models with independent data from other sites. We did not include the Bearmouth Fall model due to small sample size of locations.

<table>
<thead>
<tr>
<th>Origin of Model</th>
<th>Winter</th>
<th>Lambing</th>
<th>Fall</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Bearmouth</td>
<td>Garrison</td>
<td>Skalkaho</td>
</tr>
<tr>
<td>Bearmouth</td>
<td>0.879 $P&lt;0.001$</td>
<td>-0.200 $P=0.580$</td>
<td>0.842 $P&lt;0.001$</td>
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<tr>
<td>Garrison</td>
<td>-0.212 $P=0.556$</td>
<td>0.964 $P&lt;0.001$</td>
<td>-0.030 $P=0.934$</td>
</tr>
<tr>
<td>Skalkaho</td>
<td>0.442 $P=0.200$</td>
<td>0.879 $P&lt;0.001$</td>
<td>0.927 $P&lt;0.001$</td>
</tr>
</tbody>
</table>

Testing these models across sites produced mixed results. We excluded the Bearmouth fall data from these model comparisons due to low sample sizes; all other possible models tests were carried out (Table 4). While some models did quite well at predicting use at other sites, this was not consistent. When a model from site 1 performed well at site 2, the model from site 2 did not necessarily perform well at site 1.

Slope and distance to escape terrain were important in most models, and models do have the potential to perform well at new sites. However, mixed results warn that site-specific patterns of use and availability can also create site-specific models that perform poorly across new landscapes.
DISCUSSION

Scale of Selection

Our analysis relates to Johnson’s (1980) third-order selection of habitat within a home range. Much emphasis has been placed recently in using RSF procedures to quantify second-order selection, or the selection of home ranges within a larger landscape. Unfortunately, the dependent and gregarious nature of a sheep herd reduced our sample size of 16 sheep to 3 herd home ranges, and 3 herds is an inadequate sample to adequately address second-order selection.

A landscape scale selection probability map is not an appropriate use of these data, so our inferences are limited to selection within home ranges. We use our third-order selection models to compare selection across this sample of herds, and address how similar or different the finer-scale selection is between recently colonized herds. Our results also provide a useful example of the limitations of site-specific modeling.

Explanatory Variables of Interest

The solar radiation index proved a stronger explanatory variable than aspect. The SRI has the advantage of being a single continuous variable, and should receive more use in future GIS habitat modeling (Dicus 2002). In agreement with past bighorn sheep habitat research (Geist 1971, Tilton and Willard 1982, McCarty and Bailey 1994) and modeling (Sweanor et al. 1996, Hughes 1997, Johnson and Swift 2000, Zeigenfuss et al. 2000, Dicus 2002), we found slope and distance to escape terrain were very important habitat variables across seasons and sites. These variables appear to be universally important to bighorn sheep habitat in our study area. However, these were not the only
variables that explained variation in resource selection, and more site-specific variation occurred in other variables.

Elevation was an especially important component of all models for Garrison. The topography of this site encouraged this, because the herd’s home range existed on a small, isolated set of foothills surrounded primarily by vast, low-elevation fields. High elevation habitat in Garrison remains as open, steep, typical sheep habitat. High elevation habitat in Bearmouth and Garrison approaches thicker forest, with more gentle slopes, and these sheep find steep, open terrain at lower elevations. Models created in Garrison are likely predicting high probabilities of use in the high elevations of other sites where other variables limit sheep use.

Distance to cover type variables also revealed differences among sites. The presence of recently burned grasslands and forest only in Bearmouth and Skalkaho created obvious site-specific differences. Best models often included these cover type variables; these sheep were probably responding to effects of the fires. Such a situation cannot be modeled in an area without recent fire (Garrison) and represents another important, site-specific variable separating these areas. Areas in or near high-visibility habitats like grasslands and high-severity burned forests were generally preferred and low-visibility denser forests avoided. However, we did not detect significant selection based on horizontal visibility alone (Chapter 3, this thesis), and we are hesitant to accredit selection of cover types to their associated horizontal visibility.

We were unable to include all potential variables, and other factors like predator densities or fine-scale food quality and abundance could be important in describing selection.
Model Evaluation

Testing models with the same resubstituted data used to create them resulted in very high prediction success. Were this study limited to any one of these 3 sites, as is often the case, we would have been overly confident in our model’s power. The danger of applying such models to new landscapes is evident in our across-site test results. While some models predicted bighorn sheep use in new areas well, site-specific variation can strongly affect the external validity of habitat selection models. We encourage caution in applying local models to new areas without having adequately tested them in such situations.

Comparisons to Other Bighorn Habitat Models

Many recent efforts to use models in identifying suitable bighorn habitat are based on Smith et al.’s (1991) habitat evaluation procedure (HEP) (Hughes 1997, Johnson and Swift 2000, Zeigenfuss et al. 2000). The Smith et al. (1991) HEP was a stepwise procedure that identified core habitat based on escape terrain patches and subsequently removed areas from this core habitat that were unsuitable for other reasons (e.g. dense vegetation, close proximity to human development, close proximity to domestic sheep, high elk or cattle concentrations, and so on). Zeigenfuss et al. (2000) identified the 5 key habitat criteria upon which this HEP was based: 1) close proximity to large patches of escape terrain, 2) close proximity to water, 3) unrestricted by water or highway barriers, 4) high horizontal visibility, and 5) minimum of 150 m from human development.

The importance of slope and distance to escape terrain in our RSF models reaffirms the consideration of these variables in identifying core bighorn sheep habitat. We did not detect strong relationships between bighorn use and proximity to water or
roads. High horizontal visibility was not associated with bighorn habitat preferences in our study areas (Chapter 3, this thesis) and was not included in our models. Comparison to these HEPs is difficult because of differences in selection scale. Most bighorn sheep HEPs are developed to identify suitable bighorn home ranges within larger landscapes (Johnson’s [1980] second-order selection), while our models reflect third-order selection within home ranges. We did not find close proximities to water or distance to roads were consistent factors in selection within home ranges, but we cannot assess how these variables affected selection of home ranges within the larger landscape.

Dicus (2002) used similar logistic regression procedures to assess third-order winter habitat selection by bighorn sheep in northwest Montana. Parameters in his best winter range model were slope, distance to escape terrain, solar radiation index, snow cover, and values of cover types. These variables were similar to those found to be important in our study area and are measured at similar scales, but the signs and magnitudes of coefficients were not consistent with our models. Model testing procedures like those used to test across sites in our analyses would provide a clearer comparison.

**Future Recommendations**

A next step in this research might be to use RSF procedures to estimate second-order selection across a larger landscape of many bighorn sheep herds. Such a study would be especially meaningful if done with multiple recolonized populations such as these. Mladenoff et al.’s (1995) study of second-order selection of wolves provide an example of using 14 naturally colonized group home ranges to make inferences about future distributions. More recently, Mladenoff and Sickley (1998) discussed a set of 23
other pack home ranges that provided independent test data to further validate their model.

Singer et al. (2000) presented such a data set concerning bighorn sheep. They documented 24 colonizations of new habitat by bighorn sheep following transplants into source habitat elsewhere. They modeled the probability of colonization for different habitat patches and found that population growth rates in source herds and vegetation characteristics in corridors between source and colonized patches were important.

An RSF approach analyzing the habitat characteristics of the colonized and uncolonized patches themselves (instead of the corridor habitat) might be another valuable tool in the future of bighorn sheep habitat modeling and conservation. These approaches assume that the habitat choices dispersing sheep make are the best ones. All habitat selection analyses fall under this broad assumption that selection equates with better habitat quality and fitness (Van Horne 1983, Garshellis 2000). Another approach to bighorn modeling incorporates this problem by comparing successful and unsuccessful reintroductions (Johnson and Swift 2000). Incorporating fitness into measures of habitat quality should be a goal for all studies of wildlife and habitat, but funding and logistics make collection of such data problematic.

Thus, habitat selection techniques will remain an important tool in the future of bighorn sheep conservation. Slope and distance to escape terrain are consistent predictors across different bighorn ranges, but we encourage caution when making broad conclusions from local data.
LITERATURE CITED


APPENDIX A.

Table A1. Parameter coefficient estimates and standard errors for variables included in best logistic regression models of resource selection by season, Bearmouth, 2001-2002.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Winter</th>
<th>Lambing</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
<td>Estimate</td>
</tr>
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<td>NIM</td>
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<td>-0.0171</td>
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<td>NIM</td>
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</tr>
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</tr>
</tbody>
</table>

* NIM = not in model

Table A2. Parameter estimates and standard errors for variables included in best logistic regression models of resource selection by season, Garrison, 2001-2002.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Winter</th>
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<th>Fall</th>
</tr>
</thead>
<tbody>
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</table>

* NIM = not in model
Table A3. Parameter estimates and standard errors for variables included in best logistic regression models of resource selection by season, Skalkaho, 2001-2002.

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<tr>
<th>Variable</th>
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<th>Lambing Estimate</th>
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<td>-0.0002</td>
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</tbody>
</table>

\(^a\)NIM = not in model
Chapter 5. The status and distribution of recolonizing bighorn sheep in western Montana

Abstract: Three herds of bighorn sheep (*Ovis canadensis*) recently colonized unoccupied habitat in western Montana. The status and movements of these sheep have implications for future bighorn conservation in the state. We captured and radio-collared animals from each herd to assess population status and distribution. Disease did not appear to be a major source of mortality, but the potential for contact with domestic sheep was high. Autumn lamb:ewe ratios for each herd were relatively high. We detected large, migratory movements by rams in all 3 herds, and connectivity with another bighorn herd in at least 1 case. Ewes remained in consistent, local home ranges, which suggested that these are self-sustaining herds rather than range expansions of source populations.

INTRODUCTION

Since their dramatic decline in the late 19th century, bighorn sheep (*Ovis canadensis*) populations remain low, unstable, and heavily managed. Most herds in Montana are either remnant groups or the result of transplant efforts, because permanent dispersal by sheep is uncommon (Geist 1970, 1971). Three small herds recently appeared in previously unoccupied habitats in western Montana. This could indicate a future recolonization of Montana by bighorn sheep, potentially linking isolated populations. These small groups could also bring domestic sheep diseases to larger bighorn herds. We used radio-telemetry to assess the current status of these 3 herds. In this paper, we discuss their history, health, abundance, mortality, movements, and home ranges.
STUDY AREA and HISTORY

We studied the movements and habitat selection of bighorn sheep in 3 distinct areas in western Montana. These herds all pioneered new habitat within the past few decades; their presence, until now, was documented only by scattered sightings and surveys.

The Bearmouth herd is located in the southern Garnet range, roughly between Marcella Creek and Little Bear Creek. The first observations of sheep in this area were occasional sightings of rams in the early 1980’s, following a 1979 transplant of sheep into nearby lower Rock Creek. In 1987, 28 additional sheep were added to the lower Rock Creek herd, 15 km southwest of Bearmouth. One radio-collared ewe from this transplant (#14495/6) soon crossed the Clark Fork to the north and frequented the Garnet mountains between Wallace Creek and Van Curan Gulch. Sightings of this collared ewe and other sheep continued until reports of 12-15 sheep in the Bearmouth area became common. We captured this same radio-collared ewe again in March, 2001, and she remains in the area; she is currently over 20 years old.

Reports of bighorn sheep in Garrison also began in the early 1980’s, when 1 ram, 1 ewe, and 1 lamb were sighted by Lyn Nielsen of Montana Department of Fish, Wildlife and Parks (FWP). This herd gradually grew to occupy the northeast foothills of the Flint Creek Range between Independence Creek and Rock Creek. The nearest potential source herd is in the Lost Creek area, roughly 40 km south. It is unclear where the founders of the Garrison herd originated.
The Skalkaho herd occupies a mix of private and USFS land north of Skalkaho Creek between Newton Gulch and Fullerton Gulch. Two ewes were observed in this area in 1973, 1 year after a bighorn transplant to the Sula area, 30 km south. We have no additional information regarding sheep until 1988 when 1 ram, 1 ewe, and 1 lamb were observed by FWP. The herd was estimated at 36 animals in 1999, and an additional 27 were added in early 2000.

**CAPTURE**

We captured 19 sheep in March of 2001 using net-gunning from a helicopter (Krausman et al. 1985) in cooperation with Montana FWP and Helicopters by Oz. We collected blood, nasal, pharyngeal, and fecal samples for herd health analysis, and each captured sheep was fitted with a radio-collar including mortality signal (Bleich et al. 1990).

**Table 1.** Sample sizes of radio-collared bighorn sheep in each study site, 2001-2002.

<table>
<thead>
<tr>
<th>Site</th>
<th>Ewes</th>
<th>Rams</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bearmouth</td>
<td>2</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Garrison</td>
<td>7</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Skalkaho</td>
<td>7*</td>
<td>2</td>
<td>9*</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>16</td>
<td>5</td>
<td>21</td>
</tr>
</tbody>
</table>

*Note: Two of these Skalkaho ewes were collared during a previous translocation and were not captured in 2001.

**HERD HEALTH**

**Test Results**

FWP analyzed blood, nasal, pharyngeal, and fecal samples for various parasites, bacteria, and viral diseases (Table 2). *Pasteurella* spp. and *Mannheimia* spp. bacteria are often found in bighorn sheep and have been associated with pasteurellosis and pneumonia outbreaks in captive and wild herds (Miller et al. 1991, Foreyt et al. 1994, Bunch et al.)
1999, Cassirer et al. 2001). *Pasteurella trehalosi* (formerly *P. haemolytica*, Type T) was found in 18 of 19 samples, and *Mannheimia haemolytica* (formerly *P. haemolytica*, Type A) was found in 2 of 19 samples (Miller 2001). It is not uncommon for healthy bighorn sheep to carry these bacteria, but when combined with other environmental stressors like poor habitat or high lungworm loads, pasteurellosis can cause population crashes (Bunch et al. 1999).

Also part of the pneumonia complex are lungworms (*Protostrongylus* spp.), whose larvae can be detected in bighorn sheep feces (Bunch et al. 1999). Lungworm larvae were detected in 8 of 19 sheep, though in all but one case their presence was minimal. One ewe from Skalkaho had over 83 larvae/g of feces, which may be high enough to affect health (Neil Anderson, Montana FWP, personal communication); this ewe survived throughout the duration of the study. No lungworm larvae were detected in the Garrison herd.

**Table 2.** Results from bighorn herd health sampling of blood, nasal, pharyngeal, and fecal samples, 2001.

<table>
<thead>
<tr>
<th>Test</th>
<th>Bearmouth</th>
<th>Garrison</th>
<th>Skalkaho</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># pos</td>
<td># neg</td>
<td># pos</td>
<td># neg</td>
</tr>
<tr>
<td><em>Pasteurella trehalosi</em></td>
<td>4</td>
<td>0</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td><em>Mannheimia haemolytica</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Lungworms</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Lungworms</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td><em>Bovine Respiratory Syncytial Virus</em></td>
<td>4</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td><em>Bovine Viral Diarrhea</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td><em>Brucella abortus</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td><em>Epizootic Hemorrhagic Disease</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td><em>Infectious bovine rhinotracheitis</em></td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Leptospirosis (8 serovars)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L Autumn</td>
<td>0</td>
<td>4</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>L Bratis</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>L Canicola</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>L Grippo</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>L Hardjo</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>L Ictero</td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>L Pomona</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>L Tarras</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Parainfluenza 3</td>
<td>1</td>
<td>3</td>
<td>7</td>
<td>1</td>
</tr>
</tbody>
</table>
**Contact with Domestic Sheep**

We detected direct or likely contact between bighorn sheep and domestic sheep in several cases. A large domestic sheep ranch is present at the eastern border of the Bearmouth herd home range, and these domestics are often free ranging over large tracts of land. In early May, 2002, we located 3 domestic sheep bedded 200 m uphill from 2 bighorn ewes in the area. Another small group of domestic sheep is fenced in along Cramer Creek, about 5 km west of the Bearmouth ewes’ home range, but this area is occasionally traversed by Bearmouth rams. In 1 instance, 3 bighorn rams were seen bedded roughly 30 m uphill from the fence.

No domestic sheep exist near the Skalkaho herd home range, but there are domestic sheep 30 km south near the potential source bighorn herd in Sula. During a summer migration towards Sula, a radio-collared Skalkaho ram was seen grazing with another bighorn ram and several domestic sheep. We located this ram several times using telemetry from the ground, and in each instance he was alone and high on the ridges near Whiskey Gulch. FWP biologists expressed much concern regarding reported interactions between these rams and domestic sheep. It is their policy to remove such animals to prevent disease transmission to entire herds. A young ram was shot in the act of grazing on the domestic sheep ranch, and the radio-collared ram was shot by FWP in the Sleeping Child Creek area.

It is unclear if both rams were migrants from the Skalkaho herd, because reports of bighorn rams in the Whiskey Gulch area are common. It is probable that sheep from the Sula herd commonly visit habitat near Whiskey Gulch.
HERD ABUNDANCE and COMPOSITION

Through 18 months of ground telemetry we are confident in population estimates for the Bearmouth and Garrison areas (Table 3). Counting the Skalkaho herd remained more difficult as the ewes and lambs rarely formed large, easily counted groups. Reports of sheep in nearby Gird Creek and Sleeping Child Creek indicate the possibility of additional subgroups. Counts of ewes include yearlings which have not reached sexual maturity; this may result in conservative lamb:ewe ratios (Krausman et al. 1999).

Autumn lamb:ewe ratios of 25:100 (Douglas and Leslie 1999) and 26:100 (McQuivey 1978) have been prescribed as minimums for stable bighorn sheep populations. A highly productive herd of desert bighorn sheep in Nevada averaged lamb:ewe ratios of 40:100 over a period of 18 years (Douglas and Leslie 1999). The Skalkaho herd appeared to have the lowest ratios, but again this may be due to differences in detectability. Festa-Bianchet (1992) cautioned against using these ratios as indicators of bighorn population condition, and 2 years of data is not sufficient to assess long term productivity or viability.

Table 3. Estimates of bighorn sheep herd abundance, composition, and lamb/ewe ratios for three sites in western Montana during September, 2001 and August, 2002.

<table>
<thead>
<tr>
<th></th>
<th>Rams</th>
<th>Ewes</th>
<th>Lambs</th>
<th>Total</th>
<th>Lambs/100 Ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td>September, 2001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bearmouth</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>12</td>
<td>50</td>
</tr>
<tr>
<td>Garrison</td>
<td>16</td>
<td>27</td>
<td>12</td>
<td>55</td>
<td>44</td>
</tr>
<tr>
<td>Skalkaho*</td>
<td>24</td>
<td>27</td>
<td>11</td>
<td>62</td>
<td>41</td>
</tr>
<tr>
<td>August, 2002</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bearmouth</td>
<td>5</td>
<td>7</td>
<td>5</td>
<td>17</td>
<td>71</td>
</tr>
<tr>
<td>Garrison</td>
<td>20</td>
<td>34</td>
<td>20</td>
<td>74</td>
<td>59</td>
</tr>
<tr>
<td>Skalkaho*</td>
<td>25</td>
<td>25</td>
<td>8</td>
<td>58</td>
<td>32</td>
</tr>
</tbody>
</table>

*Note: Skalkaho counts are especially rough due to smaller group sizes and more closed habitat.
MORTALITY

We documented the mortalities of 6 radio-collared bighorn sheep during the study (Table 4). An adult Bearmouth ram died of suspected predation while in the lower Rock Creek area. All radio-collared sheep in Garrison survived throughout the study. In Skalkaho, 3 ewes died of suspected predation, and 1 ewe was hit by a car on Highway 38. A young Skalkaho ram was killed by FWP after contact with domestic sheep (see above).


<table>
<thead>
<tr>
<th>Site</th>
<th>Rams</th>
<th>Ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bearmouth</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Garrison</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Skalkaho</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

We used program MICROMORT (Heisey and Fuller 1985) and data from radio-collared animals to estimate survival rates for each herd (Table 5). We pooled data across sexes due to small sample sizes.


<table>
<thead>
<tr>
<th></th>
<th>Annual Survival</th>
<th>95% Confidence Interval</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bearmouth</td>
<td>0.800</td>
<td>(0.517, 1)</td>
<td>4</td>
</tr>
<tr>
<td>Garrison</td>
<td>1</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Skalkaho</td>
<td>0.637</td>
<td>(0.429, 0.946)</td>
<td>9</td>
</tr>
<tr>
<td>Pooled</td>
<td>0.811</td>
<td>(0.686, 0.959)</td>
<td>21</td>
</tr>
</tbody>
</table>

These results are based on small sample sizes, so confidence intervals are large. Similar variation exists in the literature concerning adult bighorn survival rates, with age and sex-specific survival ranging from 0.4 to 0.97 (Shackleton et al. 1999). Skalkaho sheep may be subject to higher mortality; only 3 of 7 ewes survived the entire study.
period, while all 7 ewes marked in Garrison survived. No data exist to quantify predator densities in these areas.

MOVEMENTS

An initial study objective was to use radio-collared sheep to detect potential movements between different herds. Migration between herds could alleviate the problems of small isolated sheep populations (Fitzsimmons and Buskirk 1997), but may also provide paths for the spread of diseases associated with domestic sheep (Foreyt and Jessup 1982, Jessup 1985, Technical Staff of the Desert Bighorn Council 1990).

Rams

We detected large migratory or exploratory movements for rams of all 3 herds. Both collared rams from Bearmouth moved to the Lower Rock Creek area soon after capture, where they were observed with bighorn sheep of this herd. One of the Bearmouth rams died in the Lower Rock Creek area, and the other migrated back and forth between Bearmouth and Rock Creek at least 3 times during the study period. This included a migration to Rock Creek during the rut in the fall of 2001. This ram was also located twice in the Wallace Creek area (near Clinton), about 20 km west of the Bearmouth herd. We detected the arrival of several new rams to the Bearmouth herd during the rut of 2001. Though these animals were unmarked, the Bearmouth group is small enough that an addition of 2-3 new rams was evident. We suspect that these rams migrated from Lower Rock Creek.

We collared just 1 ram in Garrison, and this individual remained in the Garrison area for the first year of the study. In May, 2002, a group of 10-15 rams, including the
collared individual, migrated southwest into the Flint Creek Range. After a few weeks of movement, this group of rams spent the summer and early fall near Boulder Creek, over 30 km southwest of Garrison. Sheep are known to make migratory movements to different seasonal ranges (Geist 1971), which may have been the case with this group of rams. We did not detect direct connectivity between these rams and bighorn sheep from other herds, but we have heard reports from USFS personnel of both ewes and rams in the Boulder Creek area during 2001 and 2002. The presence of ewes might indicate a recent colonization of this area, because ewes are less likely to make exploratory movements. The potential for connectivity exists between this poorly documented subgroup and the Garrison rams. The collared ram was again located in late October, 2002, midway between this summer range and Garrison (presumably the rams were returning to Garrison for the rut).

Two rams were collared in Skalkaho. One of these rams remained in the Skalkaho area during the entire study period, but the other made a large migration during the summer of 2001. After a period of movement, this ram stayed in the Whiskey Gulch area, 30 km south, for the duration of the summer. The Whiskey Gulch area is just north of a large herd of bighorn sheep near Sula. Though we did not observe contact, it is possible that this Skalkaho ram interacted with Sula bighorn sheep. After numerous reports of 2-3 bighorn rams (one of them radio-collared) grazing with a group of domestic sheep near Whiskey Gulch, FWP decided to use lethal control to prevent disease spread. The ram soon appeared with a small group of bighorn ewes and rams in Sleeping Child Creek, only 4 kilometers south of Skalkaho. Consistent reports of bighorn sheep up Sleeping Child Creek suggest another small sub-group may
permanently exist there. The collared ram was shot in the Sleeping Child Creek area in October, 2001.

Large movements were detected for all 3 herds, but only in the case of the Bearmount rams was direct contact with another established bighorn sheep herd observed. Connectivity between sheep in Skalkaho and Sleeping Child Creeks was detected, but it is unclear if these are actually separate populations. We collared only 5 rams, but detected much movement; this may be indicative of a great amount of undetected movement and migration occurring among bighorn rams in western Montana.

**Ewes**

Marked ewes did not display migratory behaviors. In Skalkaho, 1 collared ewe made a large movement (9 km) to the north during the beginning of lambing season. She returned to the Skalkaho area within a week. Ewes occasionally make such movements to mineral licks (Festa-Bianchet 1986), but the biology of this case is unclear. No other major movements were detected with collared ewes. We believe that these 3 colonized herds are independent and self-sustaining, and not range expansions of neighboring herds.

**HOME RANGES**

We used the Animal Movement extension with ArcView 3.2a to calculate 95% fixed kernel home ranges for each site and sex (Table 6). Ewes within a herd did not show independence in movements, so we pooled locations across individuals for a herd home range for each sex (Chapter 2, this thesis). Locations collected during migratory movements such as those described above were not included in home range calculations
Movements by Bearmouuth rams between Rock Creek and Bearmouuth were frequent, and we could not confidently delineate core home range from migratory locations. We included all locations for the Bearmouuth rams, resulting in a very large estimated home range area.

Table 6. Sex-specific areas (km²) of 95% fixed kernel herd home ranges for 3 herds of bighorn sheep in western Montana, 2001-2002.

<table>
<thead>
<tr>
<th></th>
<th>Rams</th>
<th>Ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bearmouth</td>
<td>238.76</td>
<td>17.31</td>
</tr>
<tr>
<td>Garrison</td>
<td>14.01</td>
<td>6.63</td>
</tr>
<tr>
<td>Skalkaho</td>
<td>24.63</td>
<td>6.28</td>
</tr>
</tbody>
</table>

Rams generally had larger home ranges than ewes (Geist 1971). Sheep in the Bearmouuth area had larger home ranges than both Skalkaho and Garrison. Large home ranges and small population size might suggest that the Bearmouuth area is poorer quality habitat than the other 2 sites, or it may be that a lack of suitable habitat reduces home range sizes in Garrison and Skalkaho. Such hypotheses cannot be adequately assessed with these data.

CONCLUSION

Each herd seems independent and currently self-sustaining. Disease was not an apparent source of mortality within these herds during the study, though contact with domestic sheep is occurring. Population sizes and survival in Garrison were high, while natural mortality was observed in Bearmouuth and Skalkaho. All herds had reasonably good lamb:ewe ratios each year. The Skalkaho herd had the highest adult mortality and lowest lamb:ewe ratios. We detected large movements by rams of all 3 herds and believe
that connectivity among these bighorn sheep populations is likely maintained by migrating males. We also believe that contact between western Montana’s bighorn and domestic sheep is possible even when domestic sheep ranches are not in close proximity to bighorn herds.

**LITERATURE CITED**


Chapter 6. Conclusion

My research has implications for local bighorn sheep (*Ovis canadensis*) management, future bighorn research, and the study of resource selection across all species.

Local Management

I detected much movement and some direct connectivity between western Montana’s bighorn sheep populations despite collaring few animals from a small selection of herds (Chapter 5, this thesis). If movement by these animals is representative of that by other bighorns in western Montana, connectivity between many herds is likely. The potential for future recolonizations seems high, and there are at least 2 areas (Sleeping Child Creek and Boulder Creek) where recent sightings indicate additional herds might already be establishing. Contact between bighorn and domestic sheep (*Ovis aries*) is also very probable given large bighorn movements, and I suspect these contacts could often go undetected. The health and security of both established and colonizing bighorn sheep populations may lie in minimizing contact with domestic sheep, and future management should address this possibility. Managers might reduce translocation efforts and instead focus their resources on maintaining healthy, existing populations. Sheep are displaying evidence that they can recolonize habitats themselves, and managers could better ensure the long-term viability of such animals by addressing disease and domestic sheep issues in the area. This may involve putting further resources into the study of disease.
Future Bighorn Research

I detected strong dependence between marked animals within a herd (Chapter 2, this thesis); these sheep are selecting resources as a herd and not as individuals. Each herd of bighorn sheep is then essentially a sample of 1. This might justify marking fewer animals within a herd for habitat studies, and I encourage *a priori* consideration of independence and sample size in project planning. I recommend that future researchers conduct studies across many herds of bighorn sheep to obtain multiple independent samples. The high degree of site-specific variation in resource selection among these 3 herds (Chapter 4, this thesis) is 1 example where studying a single site would fail to adequately address a large-scale question.

The study of resource selection will likely remain an important part of bighorn conservation. An ideal resource selection study might assess the selection of home ranges at a landscape-scale for many colonizing bighorn populations. Factors like slope and distance to escape terrain were consistently important (Chapter 4, this thesis). It appears that bighorn sheep could adapt to a wide variety of habitats given a few key variables, and these key variables might drive a successful, landscape-level model.

Habitat Modeling Approaches

Habitat models tested with the data used to create them showed excellent fit, but performed poorly in many cases when applied to new, independent datasets (Chapter 4, this thesis). Caution is warranted in the evaluation of resource selection models, and all such models should be tested at new sites, with independent data, before they can be considered valid for application in management and conservation.