

**RESEARCH TECHNIQUES, HABITAT USE, AND ECOLOGY OF NORTHERN
FLYING SQUIRRELS, AND RESEARCH TECHNIQUES AND DISTRIBUTION
OF RED SQUIRRELS IN THE BLACK HILLS NATIONAL FOREST AND
NORTHEASTERN SOUTH DAKOTA**

BY

MELISSA J. HOUGH

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

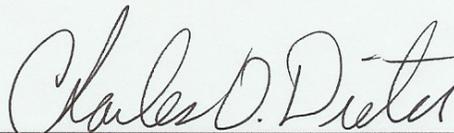
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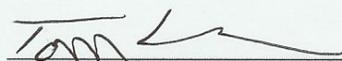
South Dakota State University

2008

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


Dr. Charles D. Dieter Date 4/22/08
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Abstract

**RESEARCH TECHNIQUES, HABITAT USE, AND ECOLOGY OF NORTHERN
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Melissa J. Hough

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This the first study conducted in northeast South Dakota and throughout the Black Hills on northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*). In northeast South Dakota there are few recent sightings of either species, and in this study neither species was captured; however, red squirrels and middens were observed. Trapping was conducted throughout the Black Hills from May through August, 2005-2007 to determine research techniques and distribution of northern flying squirrels and red squirrels. Both species were captured throughout the Black Hills, their densities differed depending on habitat characteristics. Radio-tracking was conducted on northern flying squirrels to determine design I, III, and IV (den site) resource selection (Thomas and Taylor 1990). Fifty-nine radio-collared northern flying squirrels were tracked to daytime den location every two to four weeks. The radio-collared northern flying squirrels used 133 different dens, which includes three types: drays in live trees, cavities in live trees, and cavities in snags. I compared characteristics of den trees to

random trees and available trees within the northern flying squirrels' home ranges [design IV resource selection (Thomas and Taylor 1990)]. Sixty-eight percent of dens used were in cavities. Snags and larger trees were selected for den sites more than expected based on availability. Minimum convex polygon (MCP) home ranges were determined for all radio-collared squirrels with ≥ 15 radio-tracking locations ($n = 49$). Males (11.23 ± 1.48 ha) occupied a larger area than females (6.91 ± 0.94 ha) ($P = 0.02$). Using the radiotelemetry data and GIS vegetation layers, habitat use (grass-shrub, aspen-birch, bur oak, and pine) and structural stage class (1, 3A, 3B, 3C, 4A, 4B, and 4C) selection were determined for all squirrels with ≥ 10 radio-tracking locations ($n = 54$). Selection was determined by comparing the proportion of radio-tracking locations (observed) within each habitat to the proportion within the study area (available) within each home range using techniques developed by Neu et al. (1974) [design III resource selection study (Thomas and Taylor 1990)]. Habitat use within home ranges was evaluated on the basis of foraging locations, because the majority of radio-tracking points were collected during the squirrels' nighttime active period. Northern flying squirrels selected pine habitat, while avoiding aspen-birch and bur oak. Northern flying squirrels also selected areas with larger trees and more canopy cover within the structural stage classes. A resource selection function (RSF) habitat model was created for northern flying squirrel distribution throughout the Black Hills. Logistic regression was used to compare habitat variables at used locations (observed radio-tracking and trapping locations) to a random sample of available sites throughout the study area [design I resource selection methods (Thomas and Taylor 1990)]. The RSF map delineated important areas of habitat use by

northern flying squirrels throughout the Black Hills and can be used for management purposes, as well as a baseline for future research.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	iii
ABSTRACT.....	v
LIST OF TABLES.....	x
LIST OF FIGURES.....	xii
LIST OF APPENDICES.....	xv
 CHAPTER 1 – INTRODUCTION AND STUDY AREA	
Introduction.....	1
Study area.....	5
 CHAPTER 2 – RESEARCH TECHNIQUES AND DISTRIBUTION OF NORTHERN FLYING SQUIRRELS AND RED SQUIRRELS IN SOUTH DAKOTA	
Abstract.....	13
Introduction.....	14
Methods.....	16
Results.....	21
Discussion.....	24
Management Implications.....	33
 CHAPTER 3 – DEN USE BY NORTHERN FLYING SQUIRRELS IN THE BLACK HILLS, SOUTH DAKOTA	
Abstract.....	44
Introduction.....	45
Methods.....	46

Results.....	50
Discussion.....	52
Management Implications.....	56
CHAPTER 4 – HOME RANGE AND HABITAT USE OF NORTHERN FLYING SQUIRRELS IN THE BLACK HILLS, SOUTH DAKOTA	
Abstract.....	65
Introduction.....	66
Methods.....	67
Results.....	70
Discussion.....	72
Management Implications.....	75
CHAPTER 5 – RESOURCE SELECTION HABITAT MODEL FOR NORTHERN FLYING SQUIRRELS IN THE BLACK HILLS, SOUTH DAKOTA	
Abstract.....	87
Introduction.....	87
Methods.....	89
Results.....	94
Discussion.....	96
CHAPTER 6 – CONCLUSIONS.....	110
LITERATURE CITED.....	114

LIST OF TABLES

Table 2-1. Number of northern flying squirrels (NFS) and red squirrels (RS) captured in ground traps and tree traps May–August, 2005 in the Black Hills, South Dakota.....	35
Table 2-2. Number of northern flying squirrels (NFS) and red squirrels (RS) captured in Tomahawk and Havahart live traps May–August, 2006 and 2007 in the Black Hills, South Dakota.....	36
Table 2-3. Number of captures and trapping success for northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....	37
Table 2-4. Comparison of sex ratios for northern flying squirrels (NFS) and red squirrels (RS) May-August, 2005-2007 in the Black Hills, South Dakota.....	38
Table 2-5. Comparison of male and female mass for northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....	39
Table 3-1. Number of dens used per month and distances between consecutive dens used by male and female northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....	58
Table 3-2. Description of habitat variables measured for analysis of den characteristics of northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....	59
Table 3-3. Comparison of habitat characteristics between den sites and random sites and den sites and available sites May-August, 2005-2007 in the Black Hills, South Dakota. See Table 2 for description of variables.....	60
Table 4-1. Minimum convex polygon (MCP) core areas (50%) and home ranges (100%) by year and sex for northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....	77
Table 4-2. Continuous variables tested for differences between means of northern flying squirrel tracking locations (1243 points) and hectares available within home ranges (414 ha) during May-August, 2005-2007 in the Black Hills, South Dakota. See methods for description of habitat variables.....	78
Table 4-3. Comparison of minimum convex polygon (MCP) home range sizes for northern flying squirrels across North America.....	79

Table 5-1. Description of variables considered for the resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota.....	102
Table 5-2. Chi-square tests comparing means of tracking locations (used) (n = 1203) and random locations throughout the study area (available) (n = 1203) to determine continuous variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.....	103
Table 5-3. Fisher's exact test comparing proportion of tracking locations (used) (n = 1203) and random locations throughout the study area (available) (n = 1203) to determine categorical variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.....	104
Table 5-4. Estimated coefficients for the resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.....	105
Table 5-5. Comparison of observed and expected frequencies for resource selection function (RSF) probability values categorized into 10 quantile bins to determine validity of RSF model. RSF values are probability of selection by northern flying squirrels in Black Hills, South Dakota based on trapping and tracking results May-August, 2005-2007.	106

LIST OF FIGURES

- Figure 1-1. Distribution of 25 subspecies of northern flying squirrels (*Glaucomys sabrinus*) throughout North America. The subspecies found in the Black Hills is *Glaucomys sabrinus bangsi* (2) (adapted from Wells-Gosling and Heaney 1984).....9
- Figure 1-2. Distribution of 25 subspecies of red squirrel (*Tamiasciurus hudsonicus*) throughout North America (adapted from Hall 1981). The subspecies found in the Black Hills is *Tamiasciurus hudsonicus dakotensis* (4). The subspecies found in northeast South Dakota is *Tamiasciurus hudsonicus minnesota* (15) (adapted from Steele 1998).....10
- Figure 1-3. Location of trap sites for northern flying squirrels and red squirrels in northeast South Dakota and the Black Hills, 2005-2007. Custer State Park (CSP) and Wind Cave National Park (WCNP) are located in the southeast portion of the Black Hills.....11
- Figure 1-4. Geologic map of the South Dakota and Wyoming Black Hills (adapted from Larson and Johnson 1999).....12
- Figure 2-1. Trap station, tree trap and ground trap, of Tomahawk traps (Model 201: 40x13x13cm) set for capturing northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota and December 2005 and June 2006 in northeast South Dakota.....40
- Figure 2-2. Radio-collar used for northern flying squirrel study from 2005-2007 in the Black Hills, South Dakota.....41
- Figure 2-3. Radio-collar used for red squirrel study in 2006 and 2007 in the Black Hills, South Dakota.....42
- Figure 2-4. Comparison of trapping success for northern flying squirrels and red squirrels between months May-August, 2005-2007 in the Black Hills, South Dakota.....43
- Figure 3-1. Proportion of live trees (n = 76) and snags (n = 57) used as dens by northern flying squirrels compared to available live trees (n = 3,104) and snags (n = 262) May-August, 2005-2007 in the Black Hills, South Dakota. Asterisk (*) indicates tree condition was used more than expected ($P \leq 0.05$)...61
- Figure 3-2. Den category use by male (n = 73) and female (n = 60) northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.....62

- Figure 3-3. Proportion of tree species used (n = 133) compared to tree species available (n = 2,859) May-August, 2005-2007 in the Black Hills, South Dakota.....63
- Figure 3-4. Number of drays (n = 43) and cavities (n = 90) used as den sites by tree dbh size class (cm) and tree height (m) class by northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota. Asterisk indicates cavities used significantly more than drays and dash indicates cavities used significantly less than drays for each dbh and height class ($P \leq 0.05$).....64
- Figure 4-1. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).....80
- Figure 4-2. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.....81
- Figure 4-3. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of male northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).....82
- Figure 4-4. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of female northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).....83

- Figure 4-5. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of male northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.....84
- Figure 4-6. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of female northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.....85
- Figure 4-7. Proportion of eight land aspects available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations and Black Hills study area compared to the proportion of observations (radio-tracking locations) within each aspect May-August, 2005-2007 in the Black Hills, South Dakota.....86
- Figure 5-1. Fitted regression of 10 resource selection function bins for proportion of expected versus observed validating data locations ($n = 300$) for resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota.....107
- Figure 5-2. Map (30-m) depicting increasing relative probability of habitat use by northern flying squirrels May-August, 2005-2007 throughout the Black Hills, South Dakota.....108
- Figure 5-3. Map depicting high, medium, and low probability of habitat use based on resource selection function habitat model (Fig. 5-2) and dominant habitat throughout the Black Hills, South Dakota for northern flying squirrels May-August, 2005-2007.....109

LIST OF APPENDICES

Appendix 4-1. Minimum convex polygon core areas (50% MCP) and home ranges (100% MCP) of radio-tracked northern flying squirrels with ≥ 15 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Number of radio-tracking locations used to generate home range estimates is "n"127

CHAPTER 1

INTRODUCTION AND STUDY AREA

INTRODUCTION

Northern flying squirrel (*Glaucomys sabrinus* Shaw) and red squirrel (*Tamiasciurus hudsonicus*) populations occur throughout coniferous and mixed coniferous-deciduous forests in northern North America and at higher elevations of the Appalachian and Rocky Mountains (Fig. 1-1 and 1-2). There are 25 subspecies of northern flying squirrels recognized by American Society of Mammalogists (ASM). Based on similar morphological measurements between northern flying squirrel populations from the Black Hills and western Wyoming, the subspecies designation for the Black Hills is *Glaucomys sabrinus bangsi* (King 1951; Wells-Gosling and Heaney 1984). There are 27 subspecies of red squirrels recognized by ASM, with designations based on morphological data and geographic isolation (Koprowski 2005). The subspecies found in northeastern South Dakota is *Tamiasciurus hudsonicus minnesota* (Over and Churchill 1941), while the subspecies *Tamiasciurus hudsonicus dakotensis* is found throughout the Black Hills (Turner 1974).

Northern flying squirrels and red squirrels coexist throughout most of their range; however, northern flying squirrels are nocturnal (Wells-Gosling and Heaney 1984) and red squirrels diurnal (Steele 1998). Little is known about distribution, habitat use, ecology, and interactions between northern flying squirrel and red squirrel populations in South Dakota. The two squirrel species are sympatric and depend on mature coniferous

forests for den sites and food resources, such as fungi and seeds. In northeastern South Dakota, coulees, ridges, and riparian forests provide potential habitat to support northern flying squirrels and red squirrels. This area consists primarily of a mixture of deciduous tree species, but due to urbanization and agriculture these riparian forests have been fragmented. In the Black Hills, the northern flying squirrels' primary habitat consists of ponderosa pine (*Pinus ponderosa*) stands interspersed with quaking aspen (*Populus tremuloides*), and white spruce (*Picea glauca*) (Krueger 2004). Red squirrels are highly associated with coniferous trees throughout their range (Kemp and Keith 1970; Rusch and Reeder 1978).

Northern flying squirrels and red squirrels maintain the health of forests through their role in community dynamics and energy flow of forest ecosystems (Hamilton and Cook 1940). In the Pacific Northwest, northern flying squirrels are listed as a keystone species because of their importance in dispersal of mycorrhizal fungal spores and as a prey item of several terrestrial predators, including the endangered northern spotted owl (*Strix occidentalis*) (Maser et al. 1978; Carey 2000). Northern flying squirrels primarily consume hypogeous fungus fruiting bodies (truffles) that have a symbiotic relationship with tree roots. The fungal spores pass through the digestive tract of the squirrels, are excreted in the feces, and eventually leach through the soil, coming in contact with the tree roots where the symbiotic relationship begins. The fungus is important to the tree roots in providing a barrier against toxic fungus and infections and increasing the surface area of tree roots, allowing a greater absorption of water, minerals, and nutrients (Marks and Foster 1973; Cooke 1977). Trees provide fungi carbohydrates produced through

photosynthesis (Marks and Foster 1973; Cooke 1977). Pearson and Ruggiero (2003) suggested that red squirrels may be considered a keystone species because of their larderhoarding behavior. Middens produced by red squirrels serve as a storage area for seeds, add structure to managed and even-aged forests, and decaying matter in the middens provides nutrient stores (Koprowski 2005).

The USDA Forest Service and South Dakota Natural Heritage Program classify status of species according to population size and susceptibility to decline. Within the Black Hills, northern flying squirrels are considered a Species of Local Concern by the Forest Service because of the unknown status of the population (USDA Forest Service 2005). Northern flying squirrels are currently classified as S2¹ by the South Dakota Natural Heritage Program because their population is isolated and thereby considered at risk (South Dakota Game, Fish and Parks 2006). Red squirrels are not federally or locally protected in South Dakota and the South Dakota Natural Heritage Program lists the species as S5².

No studies have been conducted on either squirrel species in northeast South Dakota (Roberts and Grant counties) and observations are rare. There have been two studies conducted on northern flying squirrels in the Black Hills. Duckwitz (2001) studied northern flying squirrels in Wind Cave National Park (WCNP) in the southern Black Hills. In a pilot study for South Dakota Game, Fish and Parks, Krueger (2004) trapped northern flying squirrels throughout the northern Black Hills. However, these

¹ Imperiled because of rarity (6 to 20 occurrences or few remaining individuals or acres) or because of some factor(s) making it very vulnerable to extinction throughout its range.

² No danger of extirpation.

studies were limited to isolated areas of the Black Hills, and population characteristics of northern flying squirrels in the Black Hills are still relatively unknown. There have been no prior studies conducted on the red squirrel population in the Black Hills.

Currently there are no management plans for northern flying squirrels or red squirrels in northeast South Dakota or the Black Hills. Within the Black Hills, populations of both squirrel species seem stable, but development of a management plan is important because the populations are isolated. Koprowski (2005) cautioned that isolated populations are highly susceptible to decline in areas with a high percentage of forested land managed for timber harvest. Understanding life history characteristics, distribution, abundance, and habitat use of northern flying squirrels and red squirrels is important to developing management plans for both species in the Black Hills and northeast South Dakota.

The four primary objectives of this study were: (1) to develop effective trapping, handling, and radio-collaring techniques associated with northern flying squirrel and red squirrel populations, (2) to gain a better understanding of the ecology of northern flying squirrel and red squirrel populations in South Dakota by examining morphological characteristics, population characteristics, and distribution, (3) to identify northern flying squirrel resource requirements through second-order, third-order, and fourth-order (den site) habitat selection characteristics, and (4) to create a predictive GIS habitat model and develop management recommendations based on the habitat requirements of northern flying squirrels.

STUDY AREA

Northeast South Dakota

Trapping was conducted in northeastern South Dakota in Sica Hollow State Park (Universal Transverse Mercator [UTM] coordinates for center of study area 14N 637976 E, and 5067096 N), near Lake Traverse (UTM 14N 667003 E, 5057289 N), and near Big Stone Lake (UTM 14N 685647 E, 5029975 N) (Fig. 1-3). Northeastern South Dakota is part of Coteau des Prairie region. This region is a highland plateau with elevation ranging from 372 to 610 m. Soils consist of Seiche loam (6-50% slopes) on the sides of wooded coulees or drainages. Annual precipitation in the area is 53 cm and mean annual temperature is 5.9 °C (Schultz 1975; Miller et al. 1977). The forests are dominated by stands of bur oak (*Quercus macrocarpa*), quaking aspen, green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), elm (*Ulmus spp.*), eastern cottonwood (*Populus deltoides*), and sugar maple (*Acer saccharum*).

Black Hills

Trapping was conducted throughout the Black Hills, located in western South Dakota (UTM 13N 574719 – 641489 E, 4809979 – 4932866 N) (Fig. 1-3). The Black Hills were established as The Black Hills Forest Reserve on February 22, 1897 by President Grover Cleveland. The objective of the reserve was to protect the land against fires, wasteful lumbering practices, and timber fraud (USDA Forest Service 2005). In 1905, the land was transferred to the Forest Service and renamed the Black Hills National Forest in 1907. The Black Hills name comes from the Lakota words *Paha sapa* meaning

‘the hills that are black’. The ponderosa pine dominated hills extend 900-1200 m above the surrounding Great Plains prairie.

The Black Hills region is a unique ecosystem that has been described as a forest island amid the Great Plains grasslands (Froiland 1990). The Black Hills were formed by a mountain uplift and extend 200 km north to south and 100 km east to west, and encompass 486,000 ha. The elevation ranges from approximately 1200 meters to 2207 meters, with the forested region only extending to 2102 meters (Froiland 1990).

The Black Hills are divided into several distinct zones; central core, limestone plateau, minnelusa foothills, red valley, hogback, and gray shale foothills (Fig. 1-4). This study was conducted in the central core, limestone plateau, and minnelusa foothills zones. The central core has shallow soils and is characterized by ridges, high peaks, and deep valleys (Froiland 1990). In the northern hills, the limestone plateau provides for moist, fertile soils (Shepperd and Battaglia 2002). The southern hills are characterized by sandstone and limestone minnelusa foothills that separate the highly erodable red shale valley from the limestone plateau. This area consists of prairie interspersed with open ponderosa pine forests.

The underlying rock and soil that characterize these zones, along with elevation and climate determine the vegetation distribution throughout the Black Hills. The northern hills are at a higher elevation with more annual precipitation (61 – 66 cm) and cooler annual temperature (7.2 °C) than the southern hills (45 – 51 cm; 9.3 °C) (Shepperd and Battaglia 2002), creating a cooler and moister environment. Ponderosa pine is found throughout the Black Hills and is the most abundant tree species dominating 83% of the

landscape (USDA Forest Service 2005). Ponderosa pine dominated habitat in the northern hills has a dense understory mixture of shrubs, saplings, and small trees (e.g. bur oak). The central and southern hills are dominated by ponderosa pine, with a mixture of quaking aspen and paper birch (*Betula papyrifera*) seral species in the bottomlands and along water sources with little to no understory. Quaking aspen dominate moister environments of the central and northern hills, particularly in disturbed areas. At higher elevations of the central and northern hills, Black Hills white spruce is more abundant comprising 2% of the landscape (USDA Forest Service 2005). In the central and southern hills, spruce occurs sporadically and is commonly found along streams. Other tree species found in the Black Hills include lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), Rocky Mountain juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), green ash, boxelder, American elm (*Ulmus americana*), and eastern hop-horn-beam (*Ostrya virginiana*).

Diversity in composition and structure of vegetation in the Black Hills has decreased from natural conditions due to more than a century of silviculture management, fire suppression, and cattle-grazing (Lentile et al. 2000). Silviculture management has encouraged growth of ponderosa pine for harvesting, which has led to even-aged ponderosa pine stands. Currently, 69% of the Black Hills National Forest is suitable for timber harvest (USDA Forest Service 1996a). Historically, periodic low-intensity fires occurred throughout the Black Hills (Shepperd and Battaglia 2002), as well as occasional crown fires (Shinneman and Baker 1997). Occasional intense fires are advantageous because of increased diversity in structure due to varying ponderosa pine age classes and

diversity in composition due to opportunities for early successional species to inhabit disturbed areas. Currently, due to fire suppression more large, intense stand-replacing crown fires are occurring, such as the Jasper burn in 2000. The burn cleared approximately 33,800 ha in the southwestern Black Hills and was about 25% larger than any other fire in the Black Hills (USDA Forest Service 2005). Cattle-grazing has decreased the number of grass, forb, and shrub species, and inhibits forest succession (Shepperd and Battaglia 2002). These management practices have resulted in lower diversity, greater density and extent of even-aged ponderosa pine forests, and stands containing little to no understory compared to pre-European settlement.

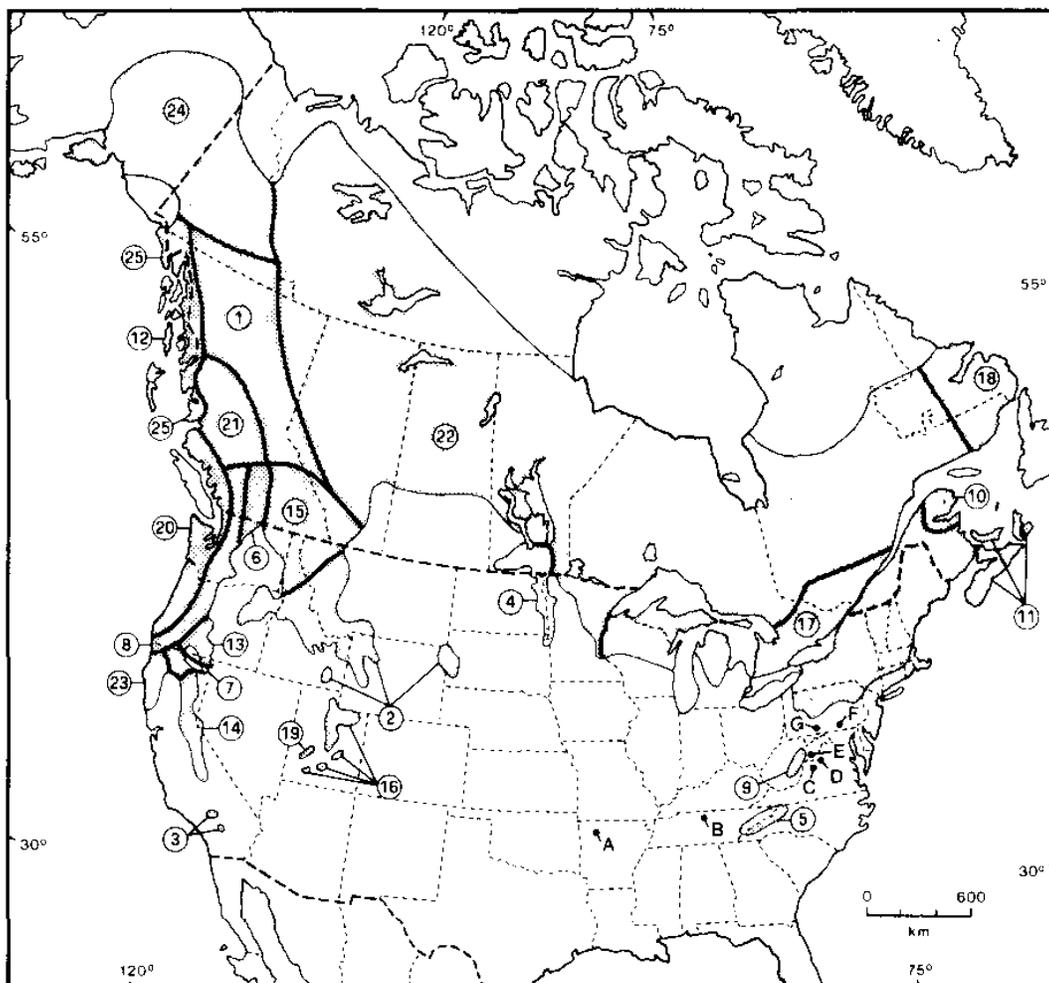


Figure 1-1. Distribution of 25 subspecies of northern flying squirrels (*Glaucomys sabrinus*) throughout North America. The subspecies found in the Black Hills is *Glaucomys sabrinus bangsi* (2) (adapted from Wells-Gosling and Heaney 1984).

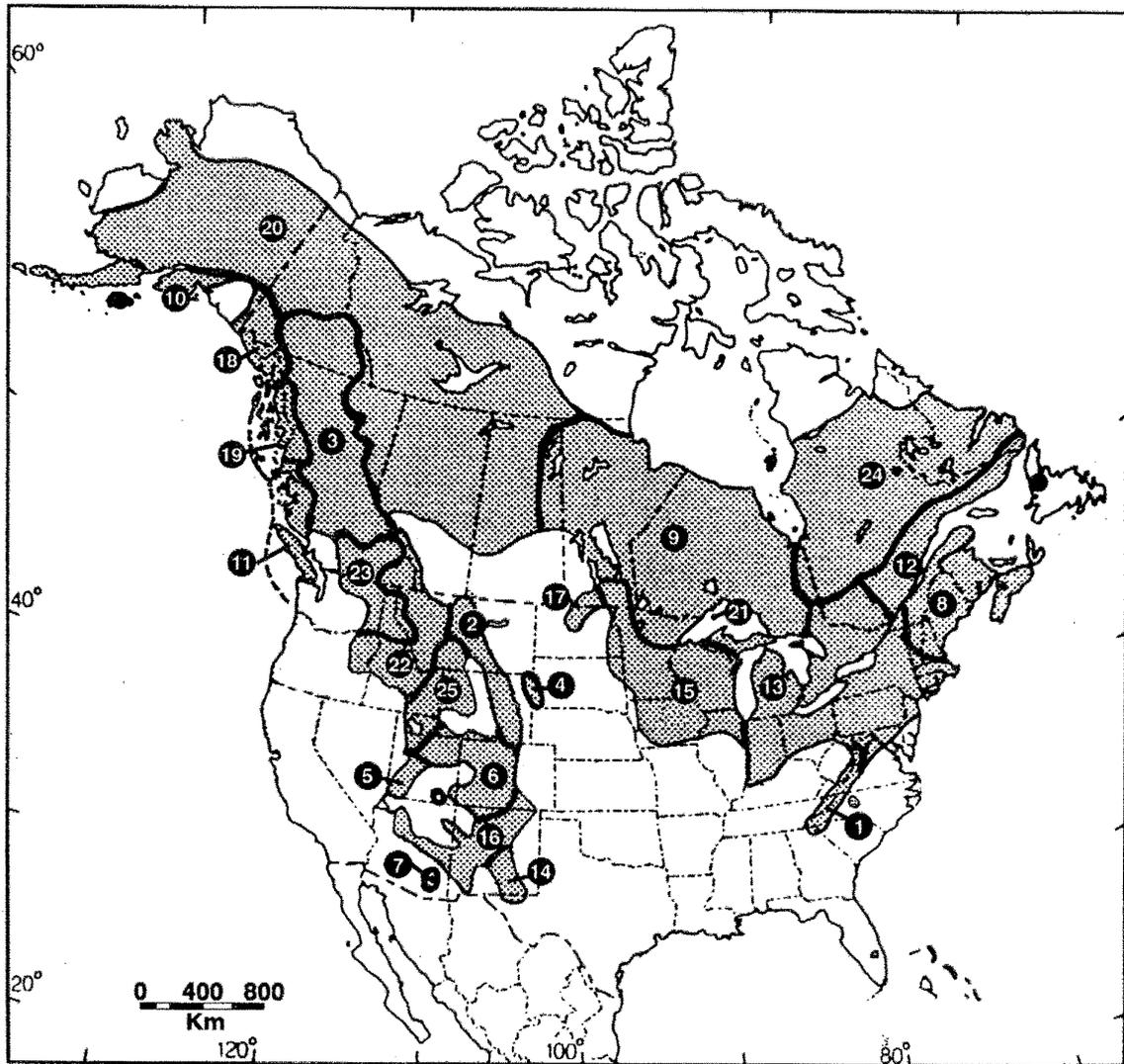


Figure 1-2. Distribution of 25 subspecies of red squirrel (*Tamiasciurus hudsonicus*) throughout North America (adapted from Hall 1981). The subspecies found in the Black Hills is *Tamiasciurus hudsonicus dakotensis* (4). The subspecies found in northeast South Dakota is *Tamiasciurus hudsonicus minnesota* (15) (adapted from Steele 1998).

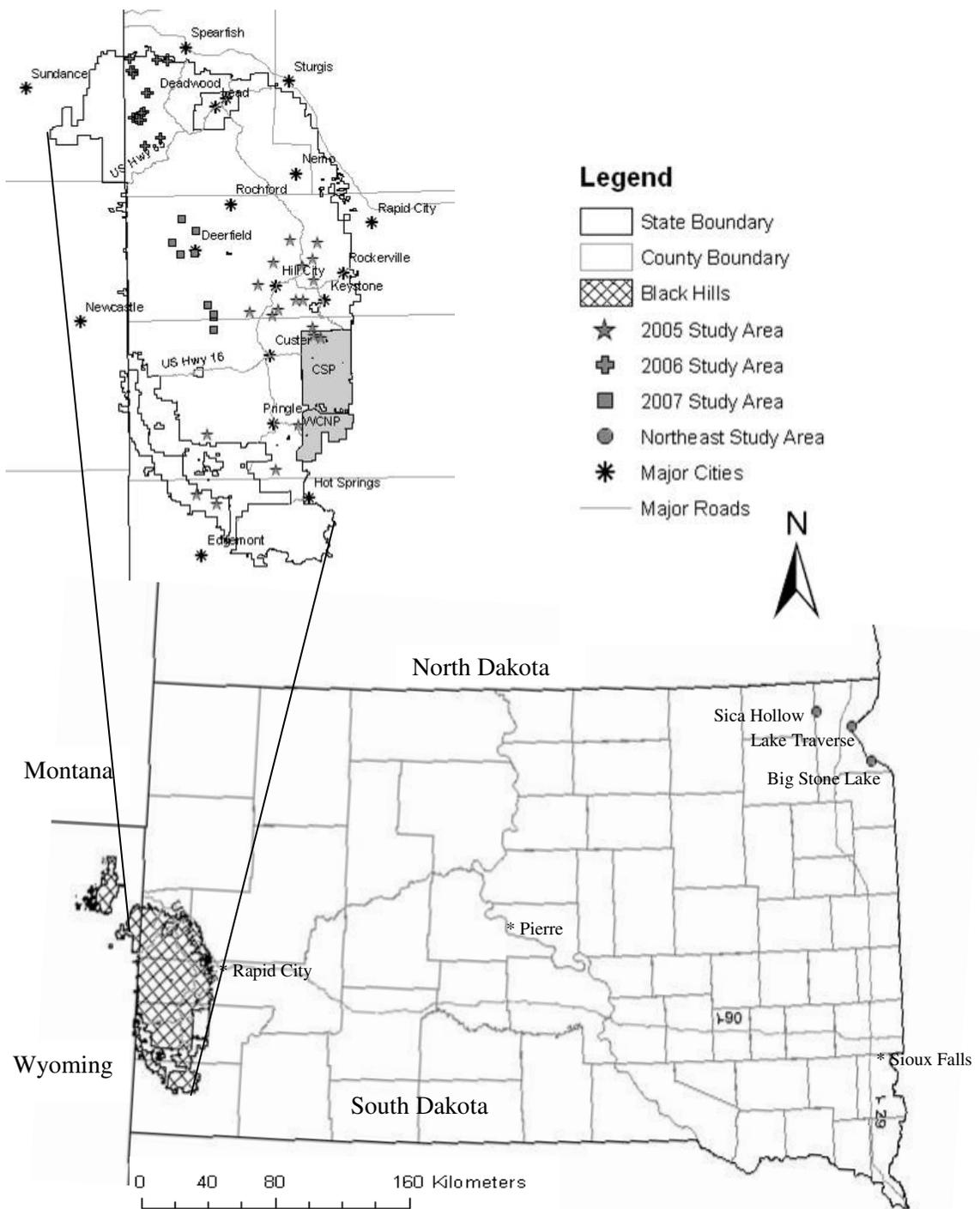


Figure 1-3. Location of trap sites for northern flying squirrels and red squirrels in northeast South Dakota and the Black Hills, 2005-2007. Custer State Park (CSP) and Wind Cave National Park (WCNP) are located in the southeast portion of the Black Hills.

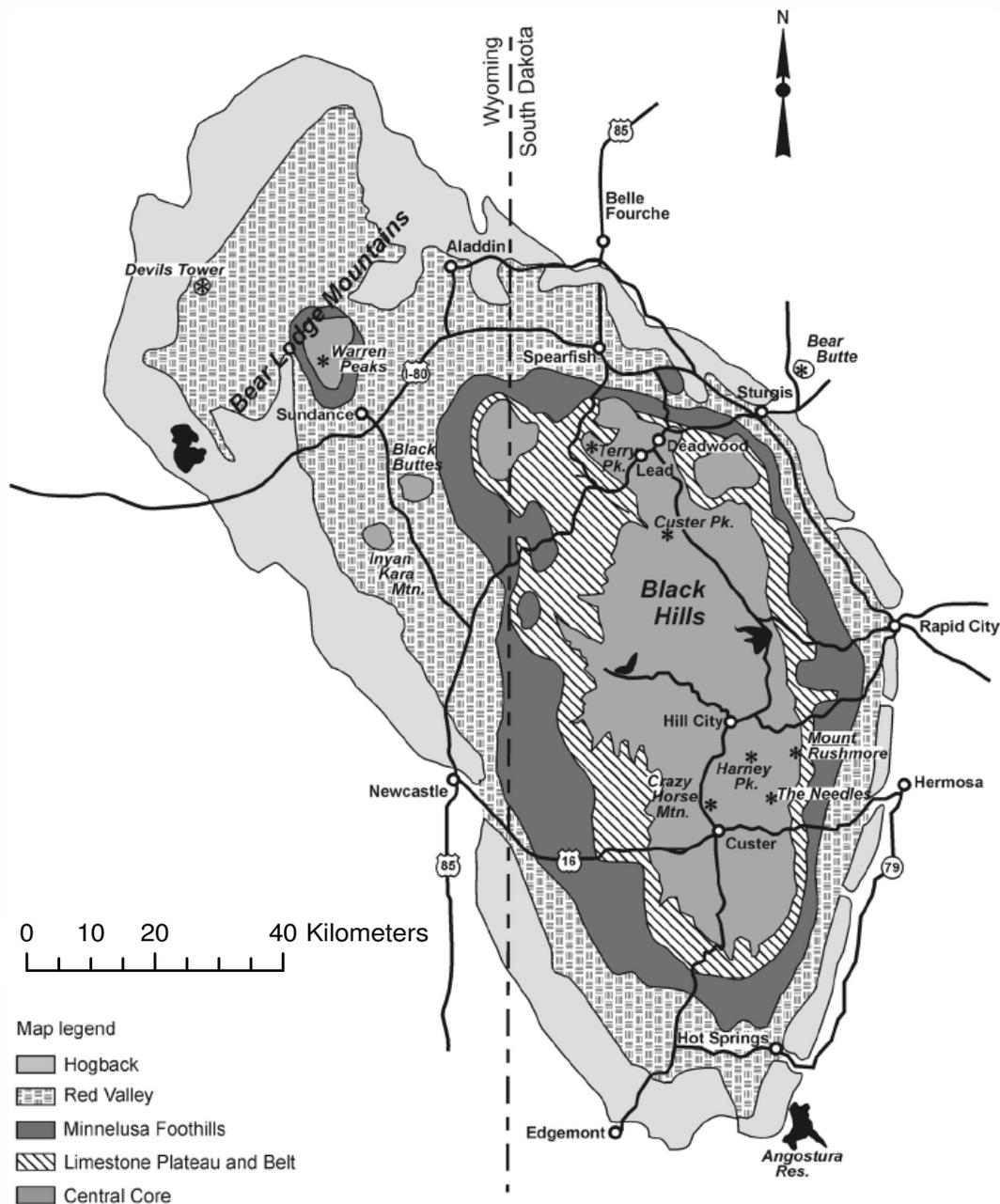


Figure 1-4. Geologic map of the South Dakota and Wyoming Black Hills (adapted from Larson and Johnson 1999).

CHAPTER 2

**RESEARCH TECHNIQUES AND DISTRIBUTION OF NORTHERN FLYING
SQUIRRELS AND RED SQUIRRELS IN SOUTH DAKOTA**

Abstract: Trapping was conducted for northern flying squirrels and red squirrels to determine presence in northeast South Dakota and distribution throughout the Black Hills. Neither squirrel species was captured in northeast South Dakota, but red squirrels and their middens were observed. While both species were captured throughout the Black Hills, their densities differed depending on habitat characteristics. Both species were captured on the edge of burned and harvested areas, which have been found to be sink habitats in other studies. Trapping techniques evaluated for northern flying squirrels were trap type, trap arrangement, trap placement, and bait. There was no difference in trap type effectiveness between Tomahawk and Havahart traps for northern flying squirrels ($P = 0.95$). Tomahawk traps were more effective than Havahart traps at capturing red squirrels ($P = 0.01$). Traps in trees were more effective than traps on ground at capturing northern flying squirrels ($P = 0.003$), but there was no difference in trap placement for red squirrels ($P = 0.08$). A mixture of peanut butter, oatmeal, and bacon grease was the most effective bait for capturing both squirrel species. Overall trapping success in the Black Hills was 2.9% for northern flying squirrels and 1.6% for red squirrels. Female northern flying squirrels (138.2 g) weighed more than males (132.4 g; $P = 0.05$), while there was no difference in mass between sexes for red squirrels ($P = 0.77$). There were similar numbers of male ($n = 56$) and female ($n = 50$) northern flying

squirrels ($P = 0.56$) captured, while more male red squirrels were captured than females ($P = 0.05$).

INTRODUCTION

Live trapping of mammals is a common practice in wildlife research to study distribution, abundance, population characteristics, and habitat associations of captured species. Four key considerations for a successful capture are trap arrangement (i.e.: line transect or grid), position (i.e.: tree or ground), trap type, and bait. Studies evaluating trapping techniques for small mammals have found a preference for trap type and method (Beachman and Krebs 1980; Whittaker et al. 1998). Using more than one trap type is recommended (Loeb et al. 1999), and traps should be placed on the ground as well as in trees for small mammal trapping (Carey et al. 1991; Loeb et al. 1999). Schemnitz (1996) found that bait is the most important factor for a successful capture.

Northern flying squirrels and red squirrels have been studied throughout their ranges, but to different degrees because of the difference in their activity periods. Northern flying squirrel research is limited, and protocols are not well developed for trapping, handling, and radio-collaring this species. In addition to being nocturnal and elusive, northern flying squirrels can be challenging to study due to capture rates as low as 1-2% (Carey et al. 1991; Adams and Campbell 1996). However, Carey et al. (1991) stated that live trapping is the most successful way to determine northern flying squirrel abundance. Red squirrel populations have been studied more extensively throughout their range, and more literature exists on red squirrel trapping techniques (Klugh 1927;

Kemp and Keith 1970; Davis and Sealander 1971; Rusch and Reeder 1978; Steele 1998; Vernes 2004).

Determining sex, reproductive status, and age of captured animals is needed to determine sex ratios, age structure, and past, current, and future population trends for the species (Dimmick and Pelton 1996). Morphological measurements on captured animals help determine if sexual dimorphism exists in populations and allows comparison of population characteristics throughout their range.

Radio-collaring is the best way to collect behavioral and ecological information for elusive and nocturnal animals (Kenward 2001). When handling wild animals, anesthesia is commonly used for easier handling and less stress to the animal and to ensure a proper fit of the radio-collar (Adams and Campbell 1996). Northern flying squirrels can be difficult to handle due to the extra skin of the patagium and because the squirrels are able to completely turn in your hands. Red squirrels are territorial and their demeanor is aggressive, so using anesthesia is also beneficial when fitting a radio-collar. The objective of this chapter was to evaluate trapping, handling, and radio-collaring methods, and determine distribution, abundance, and population characteristics of northern flying squirrel and red squirrel populations in northeast South Dakota and the Black Hills.

METHODS

Trapping

Northeast South Dakota

I set traps in coulees of Sica Hollow State Park from 13-23 December and 27-31 December 2004 along line transects by placing five trap stations of Tomahawk live traps (Fig. 2-1; Model 201: 40x13x13cm, Tomahawk Live Trap Co., Tomahawk, WI.) 50-70 meters apart. A trap station consisted of a tree trap and a ground trap. I secured traps to a tree limb with wire one to two meters off the ground and placed ground traps at the base of the same tree. I established transects parallel and perpendicular to ridges, slopes, and valleys to sample a variety of microhabitats. Transect lines cover more area, sample more microhabitats, and cover more small mammal home ranges, ultimately capturing more individual animals than a grid arrangement with the same number of traps and interval distance (Pearson and Ruggiero 2003). Pearson and Ruggiero (2003) also suggested that transect arrangement is better for species with a low capture rate.

Traps were alternately baited with tuna or a mixture of peanut butter, oatmeal, and bacon grease. I camouflaged traps using brown, green, and black spray paint and covered traps with ground litter and/or bark. Traps were winterized by wrapping cardboard and plastic around the outside and placing a small square of polyester batting inside (Vernes 2004).

For this study, a 'trap night' was considered a 24 hour day and traps were checked every morning. Traps were left open continuously to allow capturing of red squirrels

during the day and northern flying squirrels at night. I replaced the bait every three trap nights. I released all non-target captures.

Trapping was conducted in Sica Hollow State Park with the addition of riparian forests near Lake Traverse and Big Stone Lake from 24-29 July 2006. In 2006, trapping methods were changed from 2004 methods to methods that were found to be effective in the Black Hills. All traps were placed in trees 60-80 meters apart and baited with a mixture of peanut butter, oatmeal, and bacon grease. I alternated single-door Tomahawk live traps and double-door Havahart live traps (Model 1025: 45.7x12.7x12.7cm, Woodstream Corporation, Lititz, PA) to compare trap types.

Black Hills

I set traps from 9-22 May 2005 throughout the southeastern Black Hills using the same methods as those used in northeast South Dakota during December 2004. I set traps for at least 14 trap nights and checked them each morning. I changed trapping techniques from 23-30 May 2005, due to low capture rates. I substituted tuna with strawberry jam and placed ground traps and tree traps 50 m apart to increase transect length. I changed trapping techniques again from 31 May through 14 July and 11-18 August 2005 to increase capture rates. I baited all traps with a mixture of peanut butter, oatmeal, and bacon grease and increased transect length between tree traps and ground traps to 60-80 m apart to cover more area.

In 2006, I trapped in the northern Black Hills from 10 May through 14 July, and 15-25 August. In 2007, I trapped from 10 May through 24 June in the western Black Hills. During 2006 and 2007, trapping techniques were changed to methods that were

found to be effective during 2005. I placed all traps in trees and baited traps with a mixture of peanut butter, oatmeal, and bacon grease. I alternated single-door Tomahawk live traps and double-door Havahart live traps (Model 1025: 45.7X12.7X12.7cm, Woodstream Corporation, Lititz, PA) to compare trap type effectiveness for both squirrel species. To fulfill the objective of determining distribution of both species throughout the Black Hills, in 2005 traps were set in areas adjacent to recent timber harvests and in 2007 traps were set along the edge of a burn, since timber harvested and burned areas have been reported in other studies as being sink (low quality) habitats (Fisher and Wilkinson 2005).

Statistical Analysis

Fisher's exact test was used to compare trapping success between ground and tree traps for both squirrel species during 2005. Fisher's exact test was also used to test trapping success between Tomahawk and Havahart live traps for both squirrel species during 2006 and 2007. Trapping success was calculated as the number of captures per trap night. The total number of captures was divided by the number of trap nights for each year and each month. Likelihood ratio chi-square (X^2) was used to compare trapping success between years and months. Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, North Carolina) using a rejection limit of $P = 0.05$.

Captures

Each northern flying squirrel or red squirrel captured was weighed and classified as an adult or juvenile. During all three field seasons in the Black Hills, adult flying

squirrels (≥ 100 g) were fitted with Advanced Telemetry Systems (ATS; Isanti, MN) model M1610 radio transmitter collars (Fig. 2-2). The collars were made of flexible nylon for a comfortable fit and to reduce rubbing. The northern flying squirrel radio-collars were 4.0 g (2.1-3.5% of the squirrels' body mass). In the Black Hills, during 2006 and 2007, adult red squirrels (≥ 200 g) were fitted with Holohil Systems Ltd. (Ontario, Canada) model RI-2D radio transmitter collars (Fig. 2-3). A Tygon-covered wire and antenna extended out of the collar which fit around the neck of the squirrel to provide protection from rubbing and abrasions. Collars weighed approximately 9.0 g (2.4-3.7% of the squirrels' body mass). Red squirrels were collared for a related project examining the interactions of northern flying squirrel and red squirrel populations in the Black Hills. In 2005 and 2006, I encased all northern flying squirrel and red squirrel collars in epoxy mixed with cayenne pepper to deter squirrels from chewing them off (Madden and Giacalone-Madden 1982; Adams and Campbell 1996). In 2007, I omitted the epoxy mixed with cayenne pepper to test whether the squirrels would chew them off.

Adams and Campbell (1996) suggested anesthetizing northern flying squirrels to ensure a good fit of the radio-collar. With every glide the patagium pulls tight between the neck and forearm, rubbing against the collar. The collar should not fit so tightly that it rubs on the patagium or so loosely that it could lodge down over the patagium hindering the northern flying squirrel from fully extending forearms and patagium while gliding (Madden and Giacalone-Madden 1982; Adams and Campbell 1996).

Both squirrel species were anesthetized with halothane. Adult squirrels were transferred to a lidded plastic container (32x20x20cm), which served as an anesthetizing

chamber. To anesthetize squirrels, I poured 1ml of halothane into the container and monitored the squirrel for decreased breathing, closing eyes, and lethargy prior to handling them and fitting the radio-collar. I recorded the time lapse from when the halothane was added to removal of the squirrel.

For all captured squirrels (adults and juveniles) of both species, I collected hair, tissue, and blood samples for a related project analyzing DNA. I inserted a passive integrated transponder (PIT) tag (Biomark, Boise, Idaho) subcutaneously into each squirrel using a 12 gauge syringe implanter. Each PIT tag microchip had a unique number for identifying individual squirrels. I determined the sex and reproductive condition of adults by examining the condition of male scrotums and female teats (Godin 1960). Sex was not determined for juveniles. Juvenile squirrels were released after handling was completed and adult squirrels were released after they fully recovered.

Statistical Analysis

Sex ratios for adults were determined for each squirrel species and the ratios were compared to a 1:1 ratio with likelihood ratio X^2 . Wilcoxon rank sums test was used to compare mass between sexes for both squirrel species. Kruskal-Wallis test was used to compare mass of males between years and months, and mass of females between years and months for both squirrel species. Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, North Carolina) using a rejection limit of $P = 0.05$.

RESULTS

Trapping

Northeast South Dakota

In 440 trap nights, I did not capture any northern flying squirrels or red squirrels in northeast South Dakota during winter 2004 or summer 2006. However, red squirrels were seen and heard in riparian areas of Lake Traverse and Hartford Beach State Park during summer 2006. In addition, old red squirrel middens were observed near transects located in riparian areas in the northeast.

Black Hills

During 2005, I caught more northern flying squirrels in tree traps ($n = 19$) than ground traps ($n = 5$) ($X^2 = 8.71$, $P = 0.003$) (Table 2-1). There was no difference in capture rates between Tomahawk and Havahart traps for northern flying squirrels ($X^2 = 0.004$, $P = 0.95$) (Table 2-2). The capture rates between the two trap types were similar for all northern flying squirrel sex and age classes: male ($X^2 = 1.19$, $P = 0.27$), female ($X^2 = 0.02$, $P = 0.89$), adult ($X^2 = 0.67$, $P = 0.41$), and juvenile ($X^2 = 0.06$, $P = 0.81$) northern flying squirrels (Table 2-2).

During 2005, I caught more red squirrels in tree traps ($n = 29$) than ground traps ($n = 17$), but the difference was not significant ($X^2 = 3.17$, $P = 0.08$) (Table 2-1). Tomahawk traps ($X^2 = 7.99$, $P = 0.01$) had a higher capture rate for red squirrels (Table 2-2). Tomahawk live traps had a higher capture rate for male ($X^2 = 4.33$, $P = 0.04$) and adult ($X^2 = 7.92$, $P = 0.01$) red squirrels, while the two trap types had similar capture rates

for female ($X^2 = 3.62$, $P = 0.06$) and juvenile ($X^2 = 0.02$, $P = 0.88$) red squirrels (Table 2-2).

In 2005, I captured 34 northern flying squirrels with 13 recaptures in 3,489 trap nights, for a trapping success of 0.013 (Table 2-3). In 2006, I captured 97 northern flying squirrels with 80 recaptures in 4,210 trap nights, for a trapping success of 0.042 (Table 2-3). In 2007, I captured 35 northern flying squirrels with 38 recaptures in 2,624 trap nights, for a trapping success of 0.028 (Table 2-3). Overall, the trapping success was 0.029 (Table 2-3). I did not compare 2007 trapping success to 2005 and 2006 because in 2007 trapping did not occur during July and August (juvenile recruitment period). Trapping success was higher in 2006 than in 2005 ($X^2 = 59.38$, $P = <0.001$) (Table 2-3) and there was an increase in trapping success as summer progressed for northern flying squirrels ($X^2 = 93.65$, $P <0.001$) (Fig. 2-4).

In 2005, I captured 40 red squirrels with 7 recaptures in 3,489 trap nights, for a trapping success of 0.013 (Table 2-3). In 2006, I captured 17 red squirrels with 5 recaptures in 4,210 trap nights, for a trapping success of 0.005 (Table 2-3). In 2007, I captured 82 red squirrels with 12 recaptures in 2,624 trap nights, for a trapping success of 0.036 (Table 2-3). Overall, the trapping success was 0.016 (Table 2-3). I did not compare 2007 trapping success to 2005 and 2006 because during 2007 trapping did not occur during July and August. Trapping success was higher in 2005 than in 2006 ($X^2 = 92.21$, $P = <0.0001$) (Table 2-3). Trapping success during June was two times higher than trapping success during May, July, and August ($X^2 = 15.20$, $P = 0.002$) for red squirrels (Fig. 2-4).

Northern flying squirrels and red squirrels were captured on the edge of timber harvested (2005) and burned (2007) areas. Neither species was observed using the harvested or burned area. However, home ranges did extend up to the edge of the disturbed area. During 2007, even though home ranges of both squirrel species contained live trees intermixed with burned trees, the squirrels were not observed using burned trees.

Captures

The sex ratio was not different from 1:1 for captured adult northern flying squirrels (Table 2-4). Juveniles were not considered in the sex ratio analysis, because sex was not determined. During 2005, I caught six juveniles during August. During 2006, I caught 54 juveniles during July and August. During 2007, I did not capture any juveniles because trapping was not conducted during recruitment period.

During 2005 and 2006, the sex ratio for captured adult red squirrels did not differ from 1:1 (Table 2-4). However, during 2007 and when years were combined there were more adult males captured (Table 2-4). During 2005, I caught 11 juvenile red squirrels during June and July. During 2006, I caught 7 juvenile red squirrels during August. During 2007, I caught 44 juvenile red squirrels during June.

Female northern flying squirrels weighed more than males (Table 2-5). There was no difference in the mass of male northern flying squirrels between years ($X^2 = 1.98$, $P = 0.37$). During 2005 female northern flying squirrels weighed less than females in 2007 ($X^2 = 2.14$, $P = 0.03$), but no difference occurred between 2006 and 2005 ($Z = -1.85$,

$P = 0.06$) or 2007 ($Z = 0.94$, $P = 0.35$). Male ($X^2 = 3.03$, $P = 0.39$) and female ($X^2 = 6.09$, $P = 0.11$) northern flying squirrels did not fluctuate in weight between months.

Male and female red squirrels were similar in weight ($Z = 0.44$, $P = 0.77$) (Table 2-5). In 2006, male red squirrels weighed less than in 2005 ($Z = -2.67$, $P = 0.01$) and 2007 ($Z = -3.45$, $P = 0.001$). Female red squirrels were similar in mass between years ($X^2 = 0.08$, $P = 0.96$). Male red squirrels weighed less in August than the other three months of the study ($X^2 = 13.58$, $P = 0.004$), while female red squirrels did not fluctuate in weight throughout the study months ($X^2 = 0.07$, $P = 0.97$).

DISCUSSION

Northeast South Dakota

Trapping in northeast South Dakota was limited in this study. Red squirrels were seen and heard around Hartford Beach State Park and Lake Traverse in riparian forests, indicating a population exists in the area. I could not find evidence of northern flying squirrels, but in areas where they exist they often go undetected because they are nocturnal and elusive (Over and Churchill 1941; Wells-Gosling 1985). Forested regions of northeast South Dakota are patchy due to habitat degradation from agriculture and development (Turner 1974). These two squirrel species that once existed in the northeast may not exist as a resident population because of patchy distribution of suitable habitat. I recommend trapping for a longer duration and more intensively to determine abundance and distribution of red squirrels, and presence of northern flying squirrels in the area. Further trapping and observation is also needed to determine if the red squirrel population

is resident or transient. Identifying population status, habitat associations, and resource use by both species is needed for the populations in the northeast South Dakota.

Black Hills

Trapping Techniques

In recent years, there has been an increased interest in northern flying squirrels in the Pacific Northwest because of their listing as a keystone species (Maser et al. 1978; Carey et al. 1992; Carey 2000) and in the central Appalachian Mountains because of management concern over isolated and endangered populations (Weigl 1978; Payne et al. 1989; Loeb et al. 2000; Menzel et al. 2006a). However, techniques associated with capturing northern flying squirrels vary across their range. Trapping techniques were established and evaluated for northern flying squirrels in this study because of their reputation as a difficult species to trap. Literature on red squirrels does not suggest they are a difficult species to trap (Kemp and Keith 1970; Rusch and Reeder 1978; Vernes 2004).

Loeb et al. (1999) stated that some trap types are more effective at capturing small mammals. I found that Tomahawk traps were more effective than Havahart traps for capturing red squirrels, but both trap types were equally effective for northern flying squirrels. There may be several reasons why Havaharts were not as effective in capturing red squirrels. Havahart traps were double-doored, so bait was placed at each end as well as on the trip plate. I observed red squirrels steal the bait out of one side of the trap without triggering the trap and being caught. Secondly, Havahart traps must be level

when triggered in order for both doors to be locked closed; otherwise the animal will escape. It was difficult to find a level tree limb for trap placement, so I often set traps on downed limbs lodged against trees at an angle.

Trap placement is also a consideration when studying small mammal populations. Carey et al. (1991) found that successful trap placement for northern flying squirrels varied with site, season, stand type, or a combination of these factors. Even though northern flying squirrels primarily forage on the ground, traps in trees were four times more effective in my study and three times more effective in western Oregon (Witt 1991), while success varied in the coastal range of Oregon (Carey et al. 1991). Traps in trees were 34 times more effective in Texas (Engel et al. 1992) and five times more effective in Wisconsin (Taylor and Lowman 1996) over ground traps for southern flying squirrels. One possible reason traps in trees captured more northern flying squirrels may be that ground traps were already occupied by a diurnal non-target species throughout the night. The most common non-target species captured was least chipmunks (*Eutamias minimus pallidus*), which were probably captured the previous day. During 2005, bushy-tailed woodrats (*Neotoma cinerea orolestes*) were also a common non-target captured in ground traps. Trap stations are effective because chipmunks and woodrats are more likely to be captured in ground traps, thereby leaving traps in trees available for northern flying squirrels (Carey et al. 1991).

I recommend checking traps in the morning to handle northern flying squirrel captures and remove non-target species, and then checking traps again in the evening to handle red squirrel captures and remove non-target species. This method worked well

during 2005 and 2006. Red squirrel mortality is reduced using this method because red squirrels captured early in the day may not survive to the following morning due to their high metabolism and exposure to weather. However, with limited resources this method may not justify the time, money, and effort spent rechecking the traps.

Other researchers have used baits such as tuna, jam, sunflower seeds, molasses, and a mixture of peanut butter, oatmeal, and bacon grease for capturing both squirrel species (Carey et al. 1991, 2002; Wheatley et al. 2002; Menzel et al. 2004; Meyer et al. 2005). I found that a mixture of peanut butter, oatmeal, and bacon grease was most effective. Traps baited with tuna were ineffective for capturing squirrels, but attracted several nontarget carnivore and omnivore species such as pine marten (*Martes americana vulpina*), long-tailed weasels (*Mustela frenata alleni*), and striped skunks (*Mephitis mephitis*). Traps baited with strawberry jam caught several bird species, such as white-breasted nuthatch (*Sitta carolinensis*), gray jay (*Perisoreus canadensis*), and hairy woodpecker (*Picoides pubescens*).

Trapping success

There are several possible reasons for the higher trapping success for northern flying squirrels in 2006 (4.2%) compared to 2005 (1.3%). Trapping techniques were changed to decrease non-target captures and provide more opportunity for the nocturnal northern flying squirrels to use the traps. Secondly, juvenile recruitment for northern flying squirrels was earlier in 2006 than in 2005. During 2005, no juveniles were captured during 1-14 July, and juveniles were first observed at the end of July. Juveniles were regularly captured during August, 2005. During 2006, the first juvenile was

captured on 4 July and juveniles were regularly captured throughout the rest of the summer. During both years, trapping success increased as the summer progressed, but there was a marked increase during the months of juvenile recruitment. In addition, population density of northern flying squirrels in the northern hills was higher compared to the southern hills based on trapping results and my observations of uncollared squirrels. Variation in northern flying squirrel abundance within a region is due to a suite of variables and population densities increase with forest complexity (Weigl et al. 1992; Carey et al. 1999; Carey 2001).

Northern flying squirrel abundance is highest in the northern hills where more complexity and biodiversity exists within the forest. The northern hills is characterized by well-developed forest understory and more coarse woody debris, whereas the southern hills is characterized by even-aged stands (all trees are the same size) with little to no understory. Northern flying squirrel abundance has been linked to increased understory cover (Smith et al. 2004), snags, and down, dead, decaying wood (Carey et al. 1999) which add to forest complexity. Understory provides increased foraging opportunities by providing cover from predators (Carey 1995; Carey et al. 1999; Pyare and Longland 2002) and some understory species may provide food for northern flying squirrels (Smith et al. 2004). Understory species increase mycorrhizal diversity by providing more hosts (Rosentreter et al. 1997; Carey et al. 1999; Waters et al. 2000; Pyare et al. 2002).

Northern flying squirrels are also associated with snags and down woody debris (Carey et al. 1999; Smith et al. 2004). The northern hills has a higher density of both habitat features. Snags which are in higher abundance in unharvested and mature sites

provide denning locations for northern flying squirrels (Chapter 3). The lower degree of timber management for even-aged stands in the northern hills also provides a greater amount of down woody debris which provides cover, travel paths, burrow sites, and a substrate for northern flying squirrel food such as fungi and lichen (Maser et al. 1985; Carey and Johnson 1995).

These factors can be linked to increased fungal production. The primary diet of northern flying squirrels, hypogeous fungi, are associated with conifers and require moist, nutrient-rich, and cool environments to grow (Pyare and Longland 2001), such as in the northern hills. Northern flying squirrel abundance has been linked to fungus abundance (North et al. 1997; Ransome and Sullivan 1997; Carey et al. 1999; Pyare and Longland 2001) and population distribution may be heterogeneous across landscapes because of heterogeneous spatial distribution of truffles (Pyare and Longland 2002). An increase in moisture results in an increase in fungal community diversity (Carey and Johnson 1995) and abundance (Luoma et al. 1991).

Comparing years, the highest trapping success occurred during 2006 for northern flying squirrels (4.2%), while there was a marked decrease in trapping success for red squirrels (0.5%). The two squirrel species are sympatric and depend on mature coniferous forests for food resources, such as fungi and seeds. While red squirrels consume fungi, they are not as highly dependent on fungi as are northern flying squirrels. In contrast, red squirrels rely heavily on conifer seeds (Kemp and Keith 1970; Rusch and Reeder 1978) and are adapted to drier environments, such as the southern hills.

The month with highest trapping success was also the month with highest juvenile recruitment. This occurred during August (6.0%) for northern flying squirrels and during June (2.2%) for red squirrels. For northern flying squirrels, the increase in trapping success during July reflects the beginning of the juvenile recruitment period and recruitment peaks during August. Red squirrel capture success peaks during June, with a marked decrease in August.

Distribution

Northern flying squirrels and reds squirrels were trapped on the edges of burned and harvested areas, but these may be sink habitats that do not provide optimal habitat for either species (Fisher and Wilkinson 2005). Crown-burning fires are advantageous at the landscape scale in creating forest heterogeneity (Shinneman and Baker 1997). However, large scale fires that are stand-replacing are not advantageous to either tree-dependent squirrel species, because fragmented landscapes deter movement and dispersal (Fisher and Wilkinson 2005).

Burn areas do not provide adequate escape cover, food, or nesting sites for either squirrel species (Fisher and Wilkinson 2005). Stand-replacing fires do not leave sufficient canopy or ground cover for protection from predators for either squirrel species. With stand-replacing fires, mycorrhizal fungi cannot be sustained within the ecosystem because of the lack of host trees (Meyer 1973; Jasper 1994). Also, the soil environment is altered, which can reduce mycorrhizal diversity (Danielson 1984; Torres and Honrubia 1997). Coniferous seed sources are also destroyed in crown fires (Kemp and Keith 1970; Rusch and Reeder 1978). While snags for den sites are left after a burn,

the trees are not stable and do not provide conditions for food sources such as invertebrates, lichens, or fungus to exist. Red squirrels depend on large conifers for nesting, which are nonexistent after a stand-replacing fire (Fisher and Wilkinson 2005).

Crête et al. (1995) found that red squirrels and northern flying squirrels recolonize burned areas at different stand ages post fire. Non-reproductive juvenile red squirrels begin to increase in abundance within 10 years post fire, suggesting the early successional burn areas are a sink habitat for this species (Wheatley et al. 2002). Northern flying squirrels inhabit burn areas with the appearance of regenerating trees or availability of remnant trees (Fisher and Wilkinson 2005), which provide hosts for recolonizing fungal communities. A peak in both squirrel populations occurs at old-growth stages with mature seed-bearing and decaying trees, and abundant fungal and lichen growth (Fisher and Wilkinson 2005).

Northern flying squirrels and red squirrels are sensitive to tree harvest and are rarely found in recently logged sites (Fisher and Wilkinson 2005), which create the same conditions as a stand-replacing fire. Red squirrel densities decrease in clearcuts (Bayne and Hobson 1997) and significantly thinned sites (Sullivan and Moses 1986, Sullivan et al. 1996). Densities of both squirrel species increase with the age of the clearcut and uncut stands (Fisher and Wilkinson 2005).

Sexual dimorphism

My results reflected those of Rosenberg and Anthony (1992) who found female northern flying squirrels weighed more than males in western Oregon. This difference may be a reflection of the time of year trapping was conducted. In the Black Hills,

trapping occurred May through August, when females are pregnant and/or caring for young. Witt (1991) and Vernes (2004) found no difference in mass of male and female northern flying squirrels except when masses were compared during the gestation period when females were heavier than males. Females may be larger than males because caring for young involves a higher energy investment and requires females to carry more fat (Schulte-Hostedde et al. 2001). I found male and female red squirrels in the Black Hills were similar in weight reflecting the results of Vernes (2004) in New Brunswick. When I started trapping each year in May, female red squirrels were no longer pregnant.

Sex Ratio

There were no sex ratio differences for northern flying squirrels in the Black Hills. Vernes (2004) had similar results in New Brunswick. In western Oregon, Rosenberg and Anthony (1992) found no sex ratio difference for northern flying squirrels in old-growth stands, but found a higher proportion of females in second-growth stands. Rosenberg and Anthony (1992) also found more juveniles in second-growth stands and suggested these stands were sink habitats.

There were more male red squirrels trapped than females in the Black Hills. Vernes (2004) reported a sex ratio difference in favor of males during one year of study in New Brunswick. In other areas across their range, male and females juvenile red squirrel sex ratios were similar, but adult sex ratios increased in favor of males as age increased (Kemp and Keith 1970; Davis and Sealander 1971; Rusch and Reeder 1978). Higher capture rates for males may exist because males move around while females are

caring for young (Kemp and Keith 1970) or due to habitat conditions as Rosenberg and Anthony (1992) suggested for northern flying squirrels.

MANAGEMENT IMPLICATIONS

Tomahawk and Havahart live traps were equally effective in capturing northern flying squirrels, while Tomahawk traps were more effective in capturing red squirrels. I recommend Tomahawk traps because they are collapsible and lighter, therefore easier to transport in the field. Havahart traps had more bait stolen with and without the trap being triggered due to problems with setting the trap on a level surface and adjusting sensitivity of trapping mechanism. Individuals captured in Tomahawk traps were not able to escape after the trap was triggered. A disadvantage of Tomahawk traps is the wire mesh on the top of the cage which does not provide captured individuals as much protection from weather as the solid metal plate on the top of Havahart traps. I suggest covering all traps with camouflaged material and/or bark and other ground debris to provide insulation and protection from inclement weather.

There are several trapping techniques that I recommend based on results from this study. I recommend baiting traps with a mixture of peanut butter, oatmeal, and bacon grease and placing all traps in trees, because of the abundance of chipmunks and other diurnal non-target species that occupied the ground traps. Placing traps 60 to 80 meters apart ensures trap lines cover more squirrel home ranges and increases the number of original squirrels captured.

The Black Hills does not resemble historic composition and structure due to fire suppression and silviculture management. Currently, intense stand-replacing wildfires are more common than historically and silviculture practices manage for even-aged ponderosa pine stands. Areas adjacent to burns and timber harvests are highly important as refuge areas to tree-dependent wildlife. High quality habitat should be preserved in areas adjacent to fragmented landscapes to insure refuge for both squirrel species due to their dependence on trees for cover, food, and nesting.

With stand-replacing fires and clearcutting, not only does the tree community have to be reestablished, but the fungal community does as well. If fire management prescribed historical low intensity fires, the larger trees would survive, providing a host for mycorrhizal fungi to survive. While the composition of the fungi may decrease temporarily (Stendell et al. 1999), there are limited long-term effects on mycorrhizal diversity and community composition with low intensity fires (Jonsson et al. 1999). When clearcutting is prescribed, live residual trees should be left to produce future sources of downed woody material, which provides cover, travel paths, burrow sites, and a substrate for arboreal sciurid food such as fungi and lichen (Maser et al. 1985; Carey and Johnson 1995). Retention of live residual trees also facilitates maintenance of seeds, fungus, and lichens within a stand, and promotes recolonization of vegetation, fungus, and lichens in disturbed areas (Sillett and Goslin 1999). Future research should focus on studying the effects of fires and tree harvesting on the population dynamics of both squirrel species to gain a better understanding of the effects forest fragmentation and disturbances has on these isolated populations.

Table 2-1. Number of northern flying squirrels (NFS) and red squirrels (RS) captured in ground traps and tree traps May–August, 2005 in the Black Hills, South Dakota.

	Captures on Ground (n)	Captures in Tree (n)	p-value ^a
NFS	5	19	0.003
RS	17	29	0.080

^a All comparisons tested with Fisher's exact test ($P \leq 0.05$).

Table 2-2. Number of northern flying squirrels (NFS) and red squirrels (RS) captured in Tomahawk and Havahart live traps May–August, 2006 and 2007 in the Black Hills, South Dakota.

Capture	Tomahawk captures (n)	Havahart captures (n)	p-value ^a
NFS			
Adult	70	80	0.41
Male	37	47	0.27
Female	28	29	0.89
Sex Unknown	5	4	
Juvenile ^b	37	35	0.81
Age Unknown	18	11	
Total^b	125	126	0.95
RS			
Adult	39	18	0.01
Male	23	11	0.04
Female	16	7	0.06
Sex Unknown	0	0	
Juvenile ^b	24	23	0.88
Age Unknown	9	1	
Total^b	72	42	0.01

^a All comparisons tested with Fisher's exact test ($P \leq 0.05$).

^b Sex not determined for juvenile captures.

Table 2-3. Number of captures and trapping success for northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

Sampling period	Total trap nights	Northern flying squirrels		Red squirrels	
		Captures (n)	Trapping success (%)	Captures (n)	Trapping success (%)
2005					
May	1,009	2	0.20	9	0.89
June	1,430	14	0.98	24	1.68
July	700	12	1.71	14	2.00
Aug	350	19	5.43	0	0.00
Total	3,489	47	1.30	47	1.30
2006					
May	870	23	2.64	1	0.11
June	1,420	38	2.68	1	0.07
July	600	35	5.83	0	0.00
Aug	1,330	81	6.09	20	1.50
Total	4,210	177	4.20	22	0.50
2007					
May	1,374	11	0.80	30	2.18
June	1,250	62	4.96	64	5.12
Total	2,624	73	2.78	94	3.58
Total	10,333	297	2.90	163	1.60

Table 2-4. Comparison of sex ratios for northern flying squirrels (NFS) and red squirrels (RS) May-August, 2005-2007 in the Black Hills, South Dakota.

Year	NFS		RS	
	M : F	p-value ^a	M : F	p-value ^a
2005	11 : 17	0.26	16 : 13	0.58
2006	24 : 19	0.45	6 : 4	0.53
2007	21 : 14	0.24	25 : 13	0.05
Total	56 : 50	0.56	47 : 30	0.05

^a All comparisons tested with Fisher's exact test ($P \leq 0.05$).

Table 2-5. Comparison of male and female mass for northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

	Northern flying squirrel					Red squirrel				
	Male		Female		p-value ^a	Male		Female		p-value ^a
	n	mean (g)	n	mean (g)		n	mean (g)	n	mean (g)	
2005	10	135.6	17	129.6	0.52	10	263.0	5	264.3	0.92
2006	28	130.7	21	141.2	0.02	6	211.7	3	268.3	0.04
2007	15	131.9	8	146.9	0.03	18	268.6	9	263.9	0.66
Total	53	132.4	46	138.2	0.05	34	256.9	17	264.7	0.77

^a Means compared with Wilcoxon Rank Sums test ($P \leq 0.05$).



Figure 2-1. Trap station, tree trap and ground trap, of Tomahawk traps (Model 201: 40x13x13cm) set for capturing northern flying squirrels and red squirrels May-August, 2005-2007 in the Black Hills, South Dakota and December 2005 and June 2006 in northeast South Dakota.

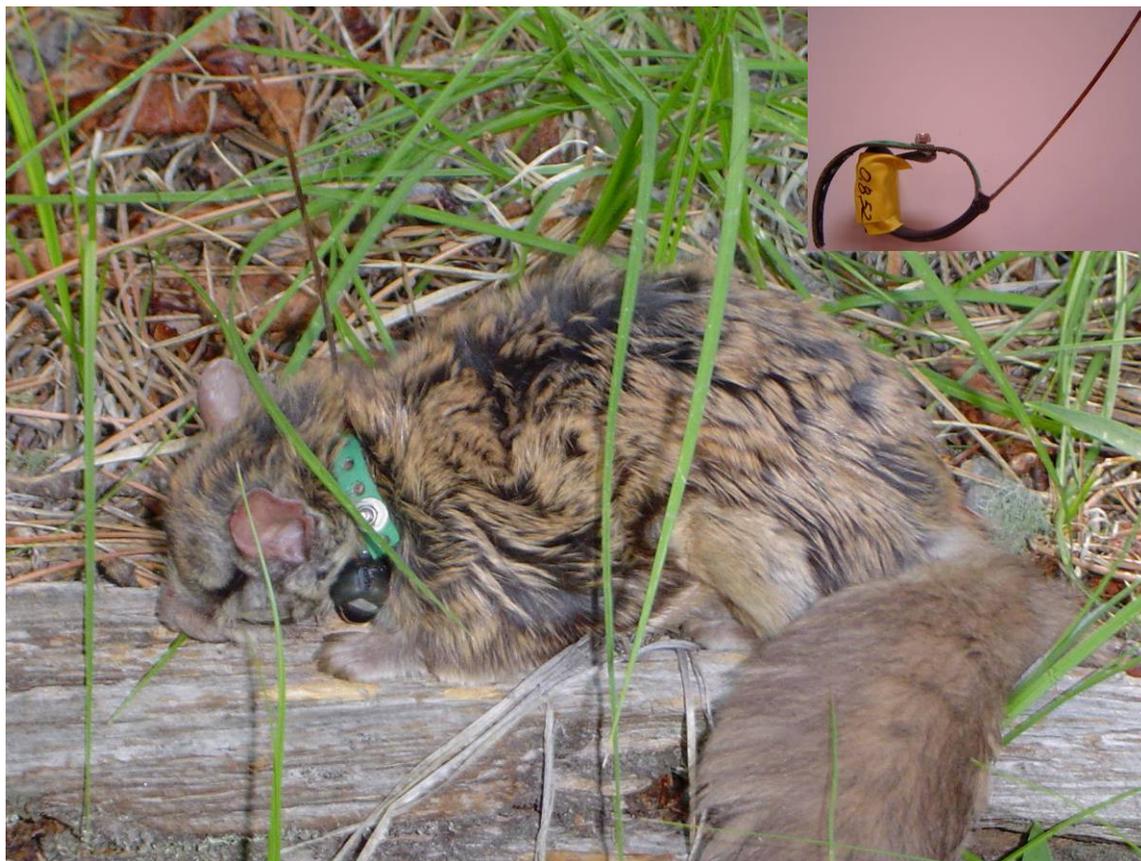


Figure 2-2. Radio-collar used for northern flying squirrel study from 2005-2007 in the Black Hills, South Dakota.



Figure 2-3. Radio-collar used for red squirrel study in 2006 and 2007 in the Black Hills, South Dakota.

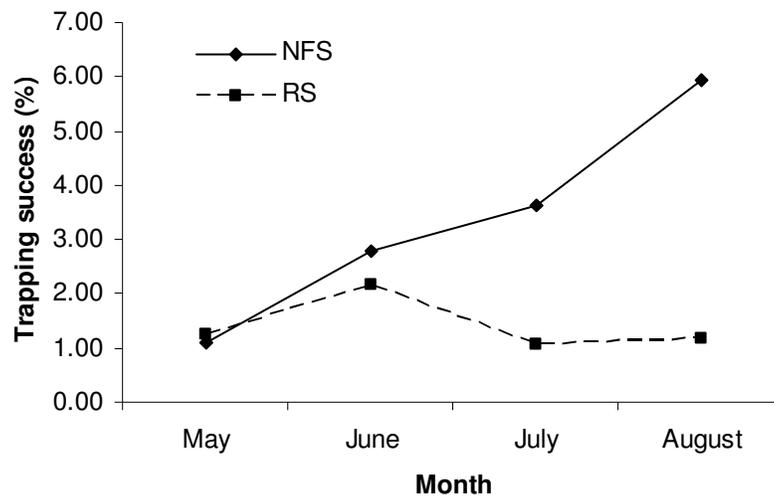


Figure 2-4. Comparison of trapping success for northern flying squirrels and red squirrels between months May-August, 2005-2007 in the Black Hills, South Dakota.

CHAPTER 3
DEN USE BY NORTHERN FLYING SQUIRRELS IN THE BLACK HILLS,
SOUTH DAKOTA

Abstract: This is the first quantitative information on denning behavior of the northern flying squirrel population in the Black Hills. Identifying habitat characteristics of dens used by northern flying squirrels is important because dens are used for daytime resting, maternal nests, and protection from weather and predators. Fifty-nine radio-collared northern flying squirrels were tracked to daytime den location every two to four weeks during May through August, 2005 through 2007. The radio-collared northern flying squirrels used 133 different dens, which included three types: drays in live trees, cavities in live trees, and cavities in snags. I compared number of dens used per month, the distance between consecutive dens used, and characteristics of den trees to random trees and available trees within the northern flying squirrels' home ranges [design IV resource selection (Thomas and Taylor 1990)]. The average number of dens used by northern flying squirrels ($n = 54$) per month was 1.16 ± 0.06 (range 0.3-2.37 dens/mo). The distance between consecutive dens was farther for males (182.93 ± 15.85 m) than females (126.17 ± 13.46 m; $Z = -2.35$, $P = 0.02$). Sixty-eight percent of the dens used were in cavities. Snags and larger trees were selected for den sites more than expected based on availability. This study will help managers understand one aspect of microhabitat resource use by northern flying squirrels in ponderosa pine dominated habitat of the Black Hills.

INTRODUCTION

Dens are a critical component of microhabitat resource use by northern flying squirrels. Dens are used for maternal nests, daytime resting locations, and protection from weather and predators. In some areas, den site availability is thought to be a limiting factor for northern flying squirrels, and snags which provide cavities are particularly important (Maser et al. 1981; Wells-Gosling and Heaney 1984).

Northern flying squirrels are secondary cavity users, occupying cavities created by woodpeckers in live or dead trees, but they also use dray nests (Wells-Gosling and Heaney 1984). Drays are external nests, similar to a typical birds nest, constructed by intertwining twigs or smaller branches and in witches' brooms. Cavities created naturally in trees from decayed branch scars are also commonly used (Thomas et al. 1979). Northern flying squirrels have been found to prefer cavities over dray nests (Carey and Sanderson 1981; Maser et al. 1981; Wells-Gosling and Heaney 1984; Bakker and Hastings 2002). Cavities and drays are lined with lichens, leaves and other materials available for insulation and the lichen serves as a food source (Wells-Gosling and Heaney 1984; Hayward and Rosentreter 1994; Carey et al. 1997).

Northern flying squirrels have been found to prefer cavities in snags and larger trees (Carey et al. 1997; Cotton and Parker 2000; Bakker and Hastings 2002; Menzel et al. 2004; Meyer et al. 2005); however other habitat characteristics of den site selection vary by region. Because of high variability in habitat measurements and range of den types and structures used within and among study areas, it has been suggested that

northern flying squirrels are not specialists in den site selection (Rosenberg and Anthony 1992; Carey et al. 1997; Cotton and Parker 2000; Hackett and Pagels 2003).

There is no information on denning behavior of northern flying squirrels in the Black Hills. The objective of this portion of the study was to determine den site characteristics selected by northern flying squirrels in the Black Hills based on design IV resource selection methods (Thomas and Taylor 1990). This information will assist managers in the Black Hills by providing microhabitat resource use and requirements of northern flying squirrels, and also contribute to the limited knowledge of northern flying squirrel denning ecology across their range.

METHODS

Tracking

To monitor den use, I located radio-collared northern flying squirrels during the day using a Yagi antenna and R2000 ATS receiver. I located daytime dens every two to four weeks and recorded the den location in Universal Transverse Mercator (UTM) coordinates with a Garmin eTrex Vista GPS (Garmin International Inc., Olathe, KS).

Number of dens used and distance between dens

I calculated the number of dens used per month for northern flying squirrels tracked at least six weeks. I used ArcMap 9.1 (Environmental Systems Research Institute Inc., Redlands, CA) to estimate the distance between UTM coordinates taken for consecutive dens used for each northern flying squirrel.

Den habitat measurements

I took habitat measurements at the den site and a tree 20 to 50 meters in a random direction from the den. I selected a random tree that was the same species as the den tree, because I wanted to eliminate potential bias due to the dominance of ponderosa pine. I wanted a direct comparison of tree characteristics and surrounding habitat characteristics for the same tree species between used dens and random trees. Habitat characteristics measured were tree species, tree condition (live or snag), den type (dray or cavity), snag decay class (adapted from Thomas et al. 1979), diameter at breast height (dbh), tree height, slope, aspect, and elevation. I measured canopy cover by averaging the percent canopy cover one meter from the tree in each of the cardinal directions.

Within a 5-m radius around the den and random tree, I recorded the sapling (<12.7 cm dbh) density, dominant sapling species, understory cover, and ground cover. Within a 10-m radius around the den and random tree I recorded total tree density, live tree density, snag density, dominant tree species, and species and dbh of all overstory live trees and snags. I recorded the height and decay class for all snags. Basal area was calculated from the dbh of trees within the 10-m radius around the den and random tree.

I could not always determine if the random tree had a cavity because some cavities are only five cm in diameter and are not obvious from the ground, so den type was not recorded for random trees. Therefore, I only analyzed differences between dens used by males and females for den type (cavity or dray) and den category (live dray, live cavity, and snag cavity).

Use versus availability

For my analyses, I compared den trees to random trees and den trees to available trees. Analyses comparing den trees to random trees compared characteristics and composition of trees within the 10-m radii around den trees and random trees, and landscape characteristics surrounding den trees and random trees. These analyses are a comparison between den sites and random sites of tree characteristics and surrounding habitat features. Throughout this chapter these comparisons are denoted as “random trees”. For other analyses, I compared characteristics of den trees to available trees. Available trees include random trees and all trees within the 10-m radii around den trees and random trees. These analyses compare characteristics of den trees to tree composition within the home ranges. Throughout this chapter these comparisons are denoted as “available trees”.

Statistical Analysis

I used Wilcoxon rank sums test to detect differences between sexes in the number of dens used per northern flying squirrel and distance between consecutive dens. I used Kruskal-Wallis test to detect differences between years in the number of dens used per northern flying squirrel and distance between consecutive dens. Fisher’s exact test was used to compare den preference for live or snag trees to available trees and den type (dray or cavity) used between sexes and years. Likelihood-ratio X^2 test was used to compare tree species used to available and categories of den types (live dray, live cavity, and snag cavity) used between sexes and years. Likelihood-ratio X^2 test was used to compare the proportion of live trees to snags used as den trees among species.

I used Wilcoxon rank sums test to detect differences in dbh and height of den trees with cavities compared to den trees with drays. Intervals were established for dbh and tree height based on current Black Hills management practices and tested with likelihood-ratio chi-square test (X^2) for significant differences in dbh and tree height intervals between trees with cavities and trees with drays.

Logistic regression was conducted to predict den use by northern flying squirrels in the Black Hills by comparing used sites and random sites. The data were subjected to a series of tests to determine which variables would be incorporated into the final model. Wilcoxon rank sums test was used to detect differences between den trees and random trees for dbh, tree height, slope, and canopy cover, and all variables measured within the 5-m radius and 10-m radius. Any categorical or continuous variables found to be significant at the 10% level were retained for further statistical analysis (Manly et al. 2002). A correlation matrix was established with retained variables when two variables were highly correlated ($r \geq 0.70$), the one deemed to be less significant biologically was removed (Manly et al. 2002). Remaining variables were incorporated into the logistic regression model. Shapiro-Wilk's test was used to test all variables for normality. Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, North Carolina) using a rejection limit of $P = 0.05$.

RESULTS

Tracking

I tracked 59 radio-collared northern flying squirrels to 133 dens (53 dens in 2005; 54 dens in 2006; 26 dens in 2007). Cavities were located in live aspen and birch trees as well as in snags of aspen, birch and pine trees. Dray nests were located in live pine and spruce trees.

Number of dens used and distance between dens

There was no difference in the number of dens used per month between sexes ($Z = 0.14$, $P = 0.89$) (Table 3-1). In 2007 northern flying squirrels used more dens per month (1.62 ± 0.13) than in 2005 (1.04 ± 0.08 m; $Z = 3.07$, $P = .002$) or 2006 (0.95 ± 0.07 m; $Z = 3.91$, $P = <0.0001$). There was no difference in the distance moved between den trees by northern flying squirrels between years ($X^2 = 0.01$, $P = 0.99$), however males (182.93 ± 15.85 m) traveled farther between dens than females (126.17 ± 13.46 m; $Z = -2.35$, $P = 0.02$) (Table 3-1). One male moved 695 m and 873 m between consecutive dens and these distances were removed as outliers.

Den tree use versus random and available trees

Northern flying squirrels in the Black Hills did not select den sites randomly ($X^2 = 125.42$, $P <0.001$). Snags ($n = 262$) comprised only 7.8% of the available trees. However, snags ($n = 57$) comprised 42.9% of the den sites and were selected almost five times more than expected based on availability ($X^2 = 113.47$, $P <0.001$) (Fig. 3-1). Tree species were selected as den trees in proportion to availability ($X^2 = 4.07$, $P = 0.40$) (Fig. 3-2). Few (<1%) live bur oak trees ($n = 20$) were available for den sites; there were no

dens in live oak trees. There were no oak snags used or available and one spruce snag was available, but none used as a den site. Therefore, only aspen, birch and pine were used to test for differences in the proportion of snags to live trees used as dens among species, and no difference was found ($X^2 = 4.40$, $P = 0.11$).

There was a difference in the number of drays and cavities used between males (18 drays and 55 cavities) and females (25 drays and 35 cavities; $X^2 = 4.35$, $P = 0.04$), but no difference between years (2005: 14 drays and 38 cavities; 2006: 18 drays and 37 cavities; 2007: 11 drays and 15 cavities; $X^2 = 1.85$, $P = 0.40$). Dens were classified into three types: dray live, cavity live and cavity snag. There was no difference in the type of dens chosen between sexes ($X^2 = 4.85$, $P = 0.09$) (Fig. 3-3) or years ($X^2 = 2.74$, $P = 0.60$).

The dbh of den trees with dray nests ($n = 43$; 36.04 ± 2.52 cm) was significantly larger than den trees with cavities ($n = 90$, 25.02 ± 0.87 cm; $Z = 4.22$, $P < 0.001$). A difference was detected in dbh classes, according to interval categories, between trees with drays and trees with cavities used as dens (Fig. 3-4). Den trees with drays ($n = 43$, 25.52 ± 1.04 m) were more than twice as tall as den trees containing cavities ($n = 90$, 11.41 ± 0.65 m; $Z = 7.97$, $P < 0.001$). When tree heights were grouped into height categories, dray nests were found in taller trees than den trees with cavities (Fig. 3-4).

Variables measured for comparison between den trees and random trees, and den trees and available trees are listed in Table 3-2. The dbh of all den trees, live trees used as dens, and snags used as dens were larger than available trees of respective tree conditions (Table 3-3). There was no difference in dbh, live tree dbh, snag dbh, snag

decay class, total tree height, live tree height, snag height, slope, aspect, elevation, or canopy cover between den trees and random trees (Table 3-3). There was no difference in density of saplings, sapling species, understory cover, or ground cover within the 5-m radius around dens and random trees (Table 3-3).

Within the 10-m radius around den trees and random trees, there was a marginal difference in the total tree basal area ($Z = 2.00$, $P = 0.05$) (Table 3-3). Within the 10-m radius around den trees and random trees, there was no difference in the dominant tree species, total tree density, total live trees, live basal area, total snags, snag basal area, total conifers, conifer basal area, total deciduous trees, or deciduous basal area (Table 3-3). Total basal area was the only variable that tested significant for use in the logistic regression model comparing den trees and random trees, so a logistic regression model predicting den use by northern flying squirrels in the Black Hills was not created.

DISCUSSION

Number of dens used and distance between dens

Northern flying squirrels have been found to change dens in response to seasonal changes in food availability or for predator avoidance (Carey et al. 1997). In the Black Hills, northern flying squirrels use fewer dens per month (one den) than what has been found in other locations. For example, northern flying squirrels used 2.1 dens in Oregon (Carey et al. 1997), 2.2 in northwestern British Columbia (Cotton and Parker 2000) and five in interior Alaska (Mowrey and Zasada 1984). However, other studies tracked during various seasons, while I only tracked during summer. Northern flying squirrels in

the Black Hills may not have changed dens as often because food resources were high during summer. Northern flying squirrels in the Black Hills also traveled farther between dens (159 m) than in Oregon (71 m) (Martin and Anthony 1999), but similar distances as in southwest Virginia (164 m) (Hackett and Pagels 2003), and northwestern British Columbia (163 m) (Cotton and Parker 2000).

During this study, males moved farther (182.9 m) between dens than females (126.2 m). This greater distance may be related to home range size as males occupy a significantly larger area than females (Martin and Anthony 1999; Cotton and Parker 2000; Meyer et al. 2005, this study chapter 4). Home ranges of male northern flying squirrels often overlap the home ranges of several females to increase male breeding potential (Carey et al. 1997). Males may travel farther between dens so they can be closest to optimal food availability within their home range, allowing for increased foraging efficiency and quick escape cover from predators (Carey et al. 1997). Females may have smaller home ranges because they care for the young and do not venture far from maternal dens. Females will change dens if the maternal den is disturbed or if there is an infestation of parasites (Carey et al. 1997). With litter sizes of two to four (Muul 1969), females choose alternate dens close to the maternal dens because of the risk and energy required to carry young between dens.

Den tree use versus availability

Northern flying squirrels in the Black Hills selected snags as den sites, as has been found in previous studies in the Sierra Nevada (Meyer et al. 2005) and central Ontario (Holloway and Malcolm 2007). While snags comprised only 6.6% of the

available trees, almost half (45.8%) of northern flying squirrel dens were located in snags. All dens in snags were in cavities, suggesting snags were selected because they contain cavities, which provide protection from weather and predators (Carey et al. 1997). Snag availability is expected to increase in the Black Hills in the coming years because of the infestation of mountain pine beetles, which kill the host tree (Shepperd and Battaglia 2002).

Females used more drays than males and males selected for cavities. When further dividing den types used, male northern flying squirrels used cavities in snags significantly more than drays or cavities in live trees, while females showed no selection. I expected females to select drays less than cavities because cavities provide better protection for maternal dens. Carey et al. (1997) suggested females that use drays in summer may have been unsuccessful in rearing young or have different parturition dates, therefore using drays early in summer but cavities later when rearing young.

In the Black Hills, all cavities in live trees were in aspen and birch trees. Northern flying squirrels are often associated with cavities in snags, however live trees with soft wood, such as aspen and birch, where cavities are readily created by primary excavators and natural formation, are frequently used as cavity den sites by northern flying squirrels (Carey and Gill 1983; Menzel et al. 2004). Cavities in live aspen and birch trees may be advantageous over cavities in snags for northern flying squirrels because the live tree provides more insulation, the canopy provides protection from weather and predators, and northern flying squirrels can use the canopy to escape (Carey et al. 1997). In addition, live trees containing cavities persist longer and are sturdier than

snags (Carey et al. 1997), likely providing the optimal maternal nesting location. The soft decaying exposed wood also provides substrate for invertebrates, lichens, fungi, and mosses (Thomas et al. 1979), which are food sources for northern flying squirrels.

Northern flying squirrels are usually generalists in den site selection, but may show a preference for snags and larger trees (Carey et al. 1997; Cotton and Parker 2000; Bakker and Hastings 2002; Meyer et al. 2005). I found similar results, with both snags and larger trees selected for den sites. Cavities are more likely to occur in larger trees because primary excavators require larger trees for nesting (Thomas et al. 1979) and larger, older trees are more prone to decay, creating cavities and snags (Lentile et al. 2000).

Drays were found in larger and taller trees, which averaged twice the height of trees containing cavities. This difference is due to the trees available for cavities. Dray nests were only found in live pine and spruce, which are the tallest tree species in the Black Hills, reaching 35 meters and 20 meters, respectively (Larson and Johnson 1999). Ponderosa pines are self-pruning, so dray nests in pines were in the top third of the tree. Taller pines provide a greater distance from ground disturbances and allow greater gliding distance for escape. Larger and taller trees containing cavities are limited in the Black Hills. Aspen and birch only grow to 15 meters (Larson and Johnson 1999) and only three pine snags were >20 m tall. Spiering and Knight (2005) found that smaller snags were common in the Black Hills and larger dbh size classes were rare (approximately 3%).

MANAGEMENT IMPLICATIONS

The Forest Service sets requirements for the minimum number and size of snags per acre for pine, spruce and other dominant overstory species, as well as green tree (live tree) retention for snag recruitment. Spiering and Knight (2005) found a high number of smaller dbh snags and few snags in the larger dbh size classes in the Black Hills. Snag densities as well as the number of cavity nesting birds have decreased from historical records (Spiering and Knight 2005). Snags in the Black Hills are used by at least 23 bird species and nine mammal species other than northern flying squirrels (Shepperd and Battaglia 2002). With the decrease in snags and available cavities, further research should be conducted to determine if the minimum standards are sufficient to support all snag-dependent wildlife species. Besides green tree retention, managing for larger size classes of pine will promote large snags over time because older trees are more prone to decay.

There are several management practices that can increase the number of cavities available. Maintaining and increasing habitat for primary cavity users is important to northern flying squirrel denning ecology because of their niche as secondary cavity users. Primary excavators in the Black Hills include several woodpecker species which nest in live aspen and birch trees (Shepperd and Battaglia 2002). Therefore, increasing the number of aspen and birch stands should increase the number of cavities. Northern flying squirrel home ranges in the BHNF include areas of aspen and birch where cavities are readily available for dens, as well as a ponderosa pine component where the fungus consumed by the northern flying squirrels readily grows. Home ranges with a mix of

aspen, birch, and pine suggests that either pine snags are not available for dens or northern flying squirrels are selecting cavities in live aspen and birch because of the advantages provided by cavities in live trees. Cavities in live aspen and birch are readily created by woodpecker excavation and natural cavities are created from detached limbs. Live aspen and birch trees with cavities should be retained because of the additional protection and resources they provide cavity users. Also, live trees persist longer and require fewer management resources (Carey et al. 1997).

In areas that are being affected by infestation of mountain pine beetles, snags should be retained to provide cavities. Snags with large dbh can be created in areas with a low density of snags. Bull and Partidge (1986) found the best technique to creating snags in ponderosa pine was to top trees at 15 to 25 meters above ground and remove lower limbs (Bull and Partridge 1986). Cavities can also be created in live trees by mechanical methods (Carey and Gill 1983). This study contributes to the knowledge of microhabitat resource use by northern flying squirrels in the Black Hills. This study also provides forest managers with information on den site requirements of northern flying squirrels in the Black Hills and stresses the importance of managing not only snags but also live hardwoods for northern flying squirrel microhabitat den use.

Table 3-1. Number of dens used per month and distances between consecutive dens used by male and female northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

	# dens used/month			Distance (m)		
	n ^a	mean \pm SE	Range	n ^b	mean \pm SE	Range
Males	31	1.18 \pm 0.10	0.30-2.37	40	182.93 \pm 15.85*	23-437
Females	23	1.13 \pm 0.07	0.67-1.68	29	126.17 \pm 13.46*	21-286
Combined	54	1.16 \pm 0.06	0.30-2.37	69	159.07 \pm 11.24	21-437

^a Number of squirrels tracked \geq 6 weeks

^b Number of distances measured between consecutive dens

* Significant difference between males and females ($P \leq 0.05$).

Table 3-2. Description of habitat variables measured for analysis of den characteristics of northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

Variable	Description
Dbh	diameter at breast height
Livedbh	diameter at breast height of live trees
Snagdbh	diameter of breast height of snag trees
Ht (m)	tree height
LiveHt (m)	tree height of live trees
SnagHt (m)	tree height of snags
Slope (%)	slope of landscape around tree
CanCov (%)	canopy cover
DenSap (n)	density of saplings within 5-m radius
UnderCov (%)	understory cover within 5-m radius
GrdCov (%)	ground cover within 5-m radius
TreesTot (n)	total number of trees within 10-m radius
TotalBA (m ²)	basal area within 10-m radius
LiveTot (n)	total number of live trees within 10-m radius
LiveDBH (n)	average dbh of live trees within 10-m radius
LiveBA (m ²)	basal area of live trees within 10-m radius
SnagTot (n)	total number of snags within 10-m radius
SnagDBH (n)	average dbh of snags within 10-m radius
SnagBA (m ²)	basal area of snags within 10-m radius
ConifTot (n)	total number of conifers within 10-m radius
ConifBA (m ²)	basal area of conifers within 10-m radius
PineTot (n)	total number of pines within 10-m radius
PineBA (m ²)	basal area of pines within 10-m radius
DecidTot (n)	total number of deciduous within 10-m radius
DecidBA (m ²)	basal area of deciduous within 10-m radius
AspBirTot (n)	total number of aspen and birch within 10-m radius
AspBirBA (m ²)	basal area of aspen and birch within 10-m radius

Table 3-3. Comparison of habitat characteristics between den sites and random sites and den sites and available sites May-August, 2005-2007 in the Black Hills, South Dakota. See Table 3-2 for description of variables.

Variable	Den			Random		Available		
	n	mean \pm SE	N	mean \pm SE	P-value ^a	n	mean \pm SE	P-value ^a
Tree(s)								
dbh (cm)	133	28.58 \pm 1.09	133	27.20 \pm 1.06	0.37	3366	23.58 \pm 0.15	<0.001*
Livedbh (cm)	76	31.34 \pm 1.61	93	28.61 \pm 1.32	0.22	3104	23.70 \pm 0.15	<0.001*
Snagdbh (cm)	57	24.90 \pm 1.23	40	23.91 \pm 1.63	0.56	262	22.07 \pm 0.53	<0.001*
Ht (m)	133	15.97 \pm 0.80	133	16.77 \pm 0.73	0.27			
LiveHt (m)	76	20.29 \pm 1.00	93	19.58 \pm 0.80	0.62			
SnagHt (m)	57	10.21 \pm 0.83	40	10.24 \pm 0.93	0.92			
Slope (%)	133	19.47 \pm 1.60	133	19.74 \pm 1.53	0.75			
CanCov (%)	133	79.24 \pm 1.92	133	80.85 \pm 1.95	0.60			
5-m radius								
DenSap (n)	133	15.21 \pm 2.29	133	12.68 \pm 2.14	0.25			
UnderCov (%)	133	16.62 \pm 2.38	133	13.67 \pm 2.23	0.13			
GrdCov (%)	133	70.15 \pm 2.78	133	66.36 \pm 3.00	0.39			
10-m radius								
TreesTot (n)	133	11.84 \pm 0.75	133	10.84 \pm 0.70	0.46			
TotalBA (m ²)	133	0.60 \pm 0.03	133	0.51 \pm 0.03	0.05			
LiveTot (n)	133	11.06 \pm 0.72	131	10.23 \pm 0.66	0.57			
LiveDBH (n)	132	20.13 \pm 0.87	129	19.05 \pm 0.76	0.40			
LiveBA (m ²)	133	0.79 \pm 0.07	133	0.70 \pm 0.06	0.14			
SnagTot (n)	133	0.78 \pm 0.12	131	0.78 \pm 0.14	0.37			
SnagDBH (n)	50	22.36 \pm 1.06	41	20.89 \pm 1.09	0.34			
SnagBA (m ²)	133	0.03 \pm 0.01	133	0.03 \pm 0.01	0.26			
ConifTot (n)	133	6.71 \pm 0.59	131	6.34 \pm 0.55	0.66			
ConifBA (m ²)	133	0.43 \pm 0.04	133	0.37 \pm 0.03	0.36			
PineTot (n)	133	6.53 \pm 0.59	131	6.11 \pm 0.56	0.67			
PineBA (m ²)	133	0.43 \pm 0.04	133	0.37 \pm 0.03	0.38			
DecidTot (n)	133	5.09 \pm 0.69	131	4.66 \pm 0.69	0.82			
DecidBA (m ²)	133	0.16 \pm 0.02	133	0.13 \pm 0.02	0.62			
AspBirTot (n)	133	5.03 \pm 0.69	131	4.59 \pm 0.69	0.81			
AspBirBA (m ²)	133	0.16 \pm 0.02	133	0.13 \pm 0.12	0.62			

^a All comparisons tested with Wilcoxon rank sums ($P \leq 0.05$).

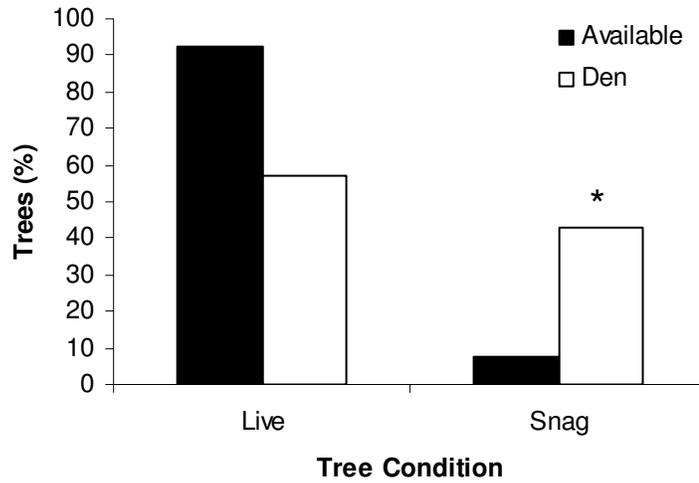


Figure 3-1. Proportion of live trees (n = 76) and snags (n = 57) used as dens by northern flying squirrels compared to available live trees (n = 3,104) and snags (n = 262) May-August, 2005-2007 in the Black Hills, South Dakota. Asterisk (*) indicates tree condition was used more than expected ($P \leq 0.05$).

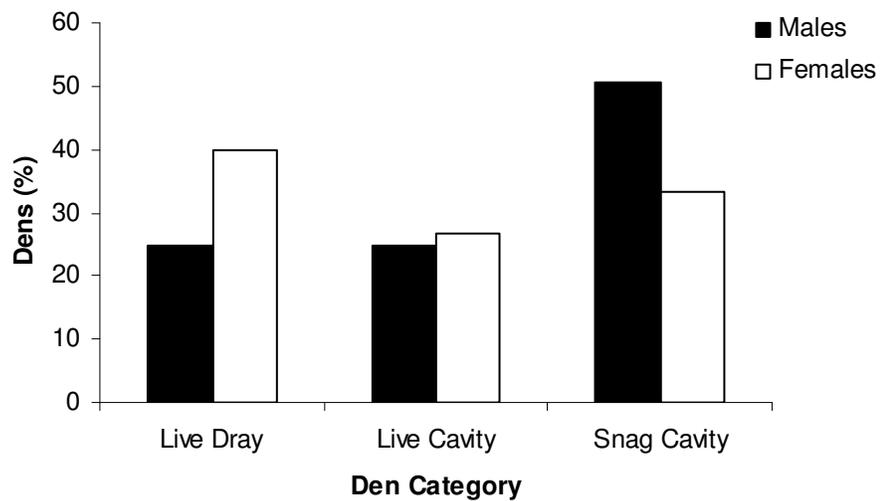


Figure 3-2. Den category use by male (n = 73) and female (n = 60) northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

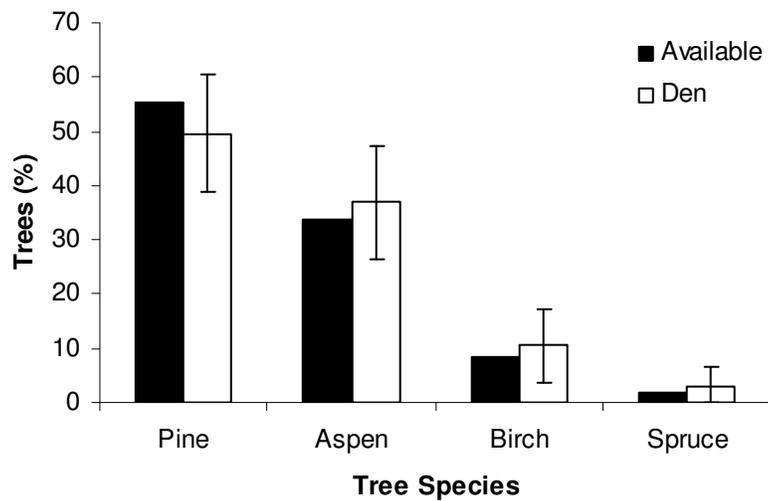


Figure 3-3. Proportion of tree species used (n = 133) compared to tree species available (n = 2,859) May-August, 2005-2007 in the Black Hills, South Dakota.

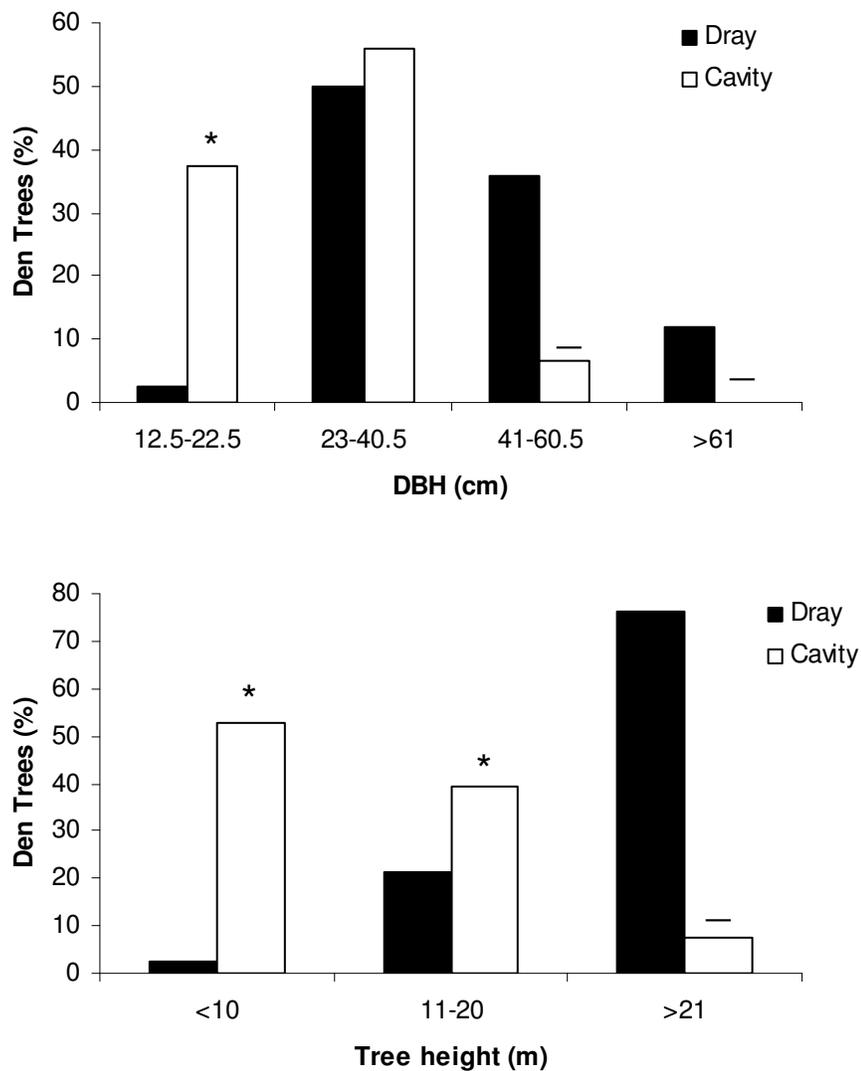


Figure 3-4. Number of drays (n = 43) and cavities (n = 90) used as den sites by tree dbh size class (cm) and tree height (m) class by northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota. Asterisk indicates cavities used significantly more than drays and dash indicates cavities used significantly less than drays for each dbh and height class ($P \leq 0.05$).

CHAPTER 4

**HOME RANGE AND HABITAT USE OF NORTHERN FLYING SQUIRRELS IN
THE BLACK HILLS, SOUTH DAKOTA**

Abstract: Home range and habitat use of northern flying squirrels in the Black Hills were studied to identify habitat requirements. Forty-nine northern flying squirrels (30 males and 19 females) were radio-collared and tracked during their active period, from dusk until dawn, by point sampling. Minimum convex polygons (MCPs) were determined from observation locations of squirrels with ≥ 15 radio-tracking locations. Males (11.23 ± 1.48 ha) occupied a larger area than females (6.91 ± 0.94 ha) ($P = 0.02$). Using the radiotelemetry data and GIS vegetation layers, habitat use (grass, aspen-birch, bur oak, and pine) and structural stage class (1, 3A, 3B, 3C, 4A, 4B, and 4C) selection were determined for all squirrels with ≥ 10 radio-tracking locations ($n = 54$). Selection was determined by comparing the proportion of radio-tracking locations (observed) within each habitat to the proportion of habitat within the MCPs (available) using techniques developed by Neu et al. (1974) [design III resource selection (Thomas and Taylor 1990)]. Habitat use was evaluated on the basis of foraging habitat, because only two to three points were daytime den locations, while the rest were nighttime locations. Overall, within home ranges northern flying squirrels selected pine habitat, while avoiding aspen-birch and bur oak. Northern flying squirrels also selected areas with larger trees and more canopy cover. Within their home ranges, northern flying squirrels were associated with more live trees >12.7 cm dbh, higher basal area of live trees, and fewer snags.

INTRODUCTION

Burt (1943) first defined home range as the area regularly used by an individual animal that includes all resources necessary for daily survival. Minimum convex polygon (MCP) home ranges are determined by connecting the peripheral radio-tracking points for each animal (Mohr 1947). Core areas (50% MCP) can also be determined by connecting the peripheral radio-tracking points that include 50% of the radio-tracking locations from the mean of the 100% MCP polygon (White and Garrott 1990).

Habitat selection can be determined by comparing the proportion of each habitat type within a home range to the proportion of radio-tracking locations within each habitat (Mohr 1947). Determining habitat selection within home ranges is a design III resource selection study (Thomas and Taylor 1990). When resources are used more than expected based on availability, selection occurs for that resource (Johnson 1980). Habitat availability is determined as the proportion of each habitat type within each radio-collared animal's minimum convex polygon (MCP) home range (Mohr 1947). Habitat use is determined as the proportion of radio-tracking points in each habitat type for each radio-collared animal. Comparing habitat use to availability determines if habitats are used randomly and ranks habitat use (Aebischer et al. 1993).

Northern flying squirrels are limited in their home range size and distribution by den site availability (Carey 1995; Carey et al. 1997) and food abundance (North et al. 1997; Carey et al. 1999; Pyare and Longland 2001; Ransome and Sullivan 1997, 2004). Northern flying squirrels depend on aspen and birch trees and snags for cavity den sites, and large, live pine and spruce trees for dray nests (Chapter 3). Northern flying squirrels

are mycophagists that primarily consume hypogeous mycorrhizal fungi. The objectives of this portion of the study were to evaluate home range size of northern flying squirrels and assess habitat selection within home ranges based on foraging resource requirements.

METHODS

Radio-tracking

I located radio-collared northern flying squirrels with a Yagi antenna and model R2000 ATS receiver. Radio-tracking was conducted from May - August 2005-2007. Radio-collared adult northern flying squirrels were tracked from dusk to dawn (8 p.m. to 5 a.m) by point sampling (Kenward 2001) to determine their home range and movement patterns. I recorded the northern flying squirrel's location every few hours to determine habitat use during their active period (Kenward 2001). I tracked squirrels throughout their active period to determine if squirrels exhibited a biphasic active period as has been reported by Weigl and Osgood (1974).

Flying squirrel locations were recorded in Universal Transverse Mercator (UTM) coordinates with a Garmin eTrex Vista GPS (Garmin International Inc., Olathe, KS). The waypoints were downloaded using Garmin MapSource (Garmin International Inc., Olathe, KS) then transferred to ArcGIS 9.1 (Environmental Systems Research Institute Inc., Redlands, CA) for analyses. All tracking locations and activity of squirrels were recorded, as well as species and condition (live or dead) of the tree which the northern flying squirrel was associated. While radio-tracking northern flying squirrels, I attempted to see each of the squirrel I was tracking to monitor behavior. I looked for reddish-

orange eye shine or flashes of white as the squirrels glided from tree to tree. I took a GPS point at the location of the original signal before the squirrel moved to avoid biasing home range calculations by forcing squirrels out of their home range. While tracking females, if young were present with the female, observational notes were taken on the size and number of young, and behavior of young and female.

Home Range

I used the Home Range Extension (Rodgers et al. 2007) in ArcGIS 9.1 to calculate 100% and 50% (core area) minimum convex polygon (MCP) home ranges for all northern flying squirrels with ≥ 15 radio-tracking points. MCPs are the most commonly used and most suitable method for comparing home ranges to other studies (Mohr and Stumpf 1966). Wilcoxon rank sums test was used to compare home range and core area size between sexes of northern flying squirrels in the Black Hills. Kruskal-Wallis test was used to compare home range and core area size between years in the Black Hills.

Habitat Use

To determine habitat selection within home ranges, I used the clip tool in ArcGIS 9.1 to extract the Black Hills vegetation layer to the 100% MCP for each northern flying squirrel with ≥ 10 tracking locations. The Forest Service has established structural classes based on canopy cover and dbh for the Black Hills National Forest (USDA Forest Service 2005). DBH class is designated by a number: 1-2 is < 2.5 cm, 3 is 2.5-23 cm, 4 is 23.1-40 cm, and 5 is > 40 cm. Canopy cover class is designated by a letter: A is 11-40%, B is 41-70%, and C is $> 70\%$. I determined the number of hectares of each habitat type (pine,

aspen-birch, bur oak, and grass-shrubs) and structural class (1-2, 3A, 3B, 3C, 4A, 4B, 4C, 5) within the MCP home range of each squirrel, and the number of tracking points located within each habitat type and structural class.

I compared the summed frequency of each available habitat type and structural class within home ranges to the frequency of points in each habitat type and structural class with likelihood ratio X^2 . When habitat types were used disproportionately to availability, Bonferroni z-statistic confidence intervals were calculated for each habitat and structural class. I determined which habitats and structural classes were selected (percent availability lower than the confidence interval) or avoided (percent availability higher than the confidence interval) (Neu et al. 1974). The X^2 test was conducted for habitat selection within home ranges on all radio-collared squirrels and also by sex, to determine if males and females selected different resources.

I compared the proportion of radio-tracking locations in each habitat to the proportion of hectares of each habitat within all home ranges for the following habitat variables: aspect, slope, # live trees/ha, # live trees >12.7 cm dbh/ha, avg basal area (m^2) of live trees/ha, avg basal area (m^2) of dead trees/ha, # snags/ha, and # down dead trees/ha. Neu et al. (1974) methods described above for detecting significant habitat and structural stage classes were used to detect significant aspect classes because aspect was measured as a nominal variable (north, northeast, east, southeast, south, southwest, west, and northwest). All other variables were continuous, so Wilcoxon rank sums test was used to test for a difference between the means of radio-tracking locations and available hectares within the home ranges. Shapiro-Wilk's test was used to test all variables for

normality. Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, North Carolina) using a rejection limit of $P = 0.05$.

RESULTS

Home Range

There were 49 northern flying squirrels with ≥ 15 radio-tracking locations between 2005 and 2007 used in the core area (50% MCP) and home range (100% MCP) analysis (Appendix 4-1). Males occupied larger core areas ($Z = -2.02$, $P = 0.04$) and 100% MCPs ($Z = -2.29$, $P = 0.02$) than females (Table 4-1). Northern flying squirrels in the northern hills (2007) occupied more than twice the area of northern flying squirrels in the southern hills (2005) ($Z = -3.25$, $P < 0.001$) and central hills (2006) ($Z = -2.98$, $P = 0.003$) (Table 4-1). In the central hills, northern flying squirrels occupied a larger area and home ranges overlapped more than in the southern hills or central hills. Core areas (50% MCP) were twice as large in the northern hills than in the southern hills ($Z = -2.49$, $P = 0.01$), but no difference was detected for the central hills ($Z = -1.80$, $P = 0.07$) (Table 4-1).

In the southern hills, males occupied a larger area than females ($Z = 2.07$, $P = 0.04$) (Table 4-1). No difference was found for home range sizes between sexes for the northern hills ($Z = -0.99$, $P = 0.32$) or western hills ($Z = 0.13$, $P = 0.89$) (Table 4-1). In the northern hills, males occupied a larger area than males in the southern hills ($Z = -2.06$, $P = 0.04$) or central hills ($Z = -2.60$, $P = 0.01$) (Table 4-1). Female home ranges were similar in size between years ($X^2 = 4.24$, $P = 0.12$) (Table 4-1).

Habitat Use

There were 54 northern flying squirrels with ≥ 10 radio-tracking locations between 2005 and 2007 used in the habitat use analysis (Appendix 4-1). Within home ranges, there was a difference in the proportion of used and available habitat types ($X^2 = 27.09$, $P < 0.0001$). No difference was found between proportion of used and available grass and shrub habitat. Aspen-birch, and bur oak were avoided and ponderosa pine was selected (Fig. 4-1). Within home ranges, there was a difference in the proportion of used and available structural stage classes ($X^2 = 17.56$, $P = 0.008$). Structural classes 1-2 and 3B were avoided, and 3C and 4B were selected (Fig. 4-2). There was no difference in proportion of used and available structural stage classes 3A, 4A, and 4C (Fig. 4-2).

Males (Fig. 4-3) and females (Fig. 4-4) exhibited avoidance and selection of habitat types. Males avoided grass and shrub, bur oak, and aspen-birch, while females avoided aspen-birch. Males and females both selected pine. Females showed no selection or avoidance of grass-shrub. Bur oak was not used by any females. Males (Fig. 4-5) and females (Fig. 4-6) exhibited avoidance and selection of structural classes. Males avoided structural class 1-2 and selected 3C and 4B. Females selected structural class 4C and showed no selection or avoidance for other structural classes. Within their home range, northern flying squirrels selected areas with more live trees > 12.7 cm, larger basal area of live trees, and less snags (Table 4-2). Aspect was used in similar proportion to availability (Fig. 4-7).

DISCUSSION

Radio-tracking

I used 15 radio-tracking points as the minimum number for calculating northern flying squirrel home ranges because radio-tracking in Black Hills terrain was done by foot. I could not use triangulation, because the radio-transmitters only had a range of about 800 meters, and steep ridges significantly decreased the range (400 m), especially in the northern hills. Pinpointing the squirrels allowed me to become familiar with areas the squirrels occupied, their home ranges, and habitat associations.

On several occasions I observed females with young. When females chattered while gliding or scampering away from me, it usually indicated the presence of young. I used a headlamp to observe young looking out from behind branches. On one occasion I tracked a female back to her den at night. As I approached the den, the female ran off with one young, while another young peered out of the cavity.

Home Range

Home range size for male and female northern flying squirrels and average home range size for the Black Hills falls mid-range of what other study areas have found (Table 4-3). Males usually occupy a significantly larger area than females (Martin and Anthony 1999; Cotton and Parker 2000; Meyer et al. 2005). Home ranges of male northern flying squirrels often overlap the home ranges of several females to increase male breeding potential (Carey et al. 1997; Martin and Anthony 1999). Males may travel farther between dens so they can be closest to optimal food availability within their home range, allowing for increased foraging efficiency and quick escape cover from predators (Carey

et al. 1997; Martin and Anthony 1999). Females may have smaller home ranges because they care for the young and do not venture far from maternal dens.

With the higher density of northern flying squirrels in the northern Black Hills (Chapter 2), I expected home range size to be similar or smaller than in the central and southern hills. However, home range size for northern flying squirrels in the northern hills was more than twice as large as the southern and central hills. Several studies on squirrels have found that home range sizes were the smallest in areas with the highest squirrel density (Gurnell 1987; Klenner and Krebs 1991; Sullivan and Sullivan 1982). The contradiction in density and home range size in the northern hills could be due to density-dependence factors for resources, such as food and den site availability. In the central and southern hills the squirrels may be limited to areas of moisture availability where fungi can readily grow, resulting in smaller home ranges.

There is limited research in the Black Hills on fungus composition, but other research has suggested that species composition changes with moisture levels as different fungi have different moisture level tolerances (Rillig et al. 2002). Northern flying squirrels in the southern hills are already restricted to areas of moisture for fungal resources, so during drought conditions they may become more generalists feeding on pine cones, nuts, berries, and fruits. The northern population can disperse to other areas of fungal occurrence. Studying fungal availability is difficult because hypogeous fungi grow underground and abundance and locations of fruiting bodies changes seasonally and annually (Fogel 1976; Hunt and Trappe 1987).

Habitat Use

Northern flying squirrels selected pine, avoided aspen-birch, and oak, and showed no selection or avoidance of grass-shrub habitats within their home ranges. Northern flying squirrels forage throughout the night, so nighttime tracking locations are assumed to be to foraging habitat. Northern flying squirrel home ranges included nighttime tracking locations (foraging locations) as well as two to four daytime tracking locations (den locations).

Pine was the only habitat selected as foraging habitat. Pine dominated habitat provides optimal foraging habitat because the two primary food source consumed by northern flying squirrels are hypogeous fungi, which is associated with conifers (Chapter 2) and pine seeds.

Aspen-birch, bur oak, and grass-shrub were not selected as foraging habitat. Aspen-birch habitat is important for denning (Chapter 3), but these trees do not provide food resources for northern flying squirrels. While bottomlands provide nutrient-rich, cool, and moist soils for fungal growth, most mycorrhizal fungi are specialists with conifers and do not have a symbiotic relationship with deciduous hardwoods, such as aspen and birch. Oak only represented 3.1% of the available habitat within home ranges, and northern flying squirrels were only observed using the habitat 0.5% of the time. Northern flying squirrels are associated with mixed conifer-hardwood forests, feeding primarily on truffles associated with conifers (Weigl 1978; Maser et al. 1985; U.S. Fish and Wildlife Service 1990), however the deciduous hardwoods are used for den sites (Weigl 1978; U.S. Fish and Wildlife Service 1990). Grass-shrub habitat would not

provide optimal foraging habitat for northern flying squirrels, because this habitat does not provide hosts for fungus growth or seed production.

Northern flying squirrels in the Black Hills selected areas with larger trees and more canopy cover within their home ranges. This selection may be related to selecting pine habitat because pine trees are larger than aspen, birch, and oak, and there are no trees on grass-shrublands. Larger trees, which are also taller, provide optimal habitat for northern flying squirrels because taller trees provide greater gliding distance for escape from predators, and larger trees were selected for den sites (Chapter 3). In addition, larger trees provide food sources through seeds and established mycorrhizal community (Fisher and Wilkinson 2005). Canopy cover is advantageous for northern flying squirrels because overstory cover protects squirrels foraging on the ground from aerial predators, but also provides an escape route from ground predators (Carey et al. 1997). Northern flying squirrels were associated with areas with a lower density of snags within home ranges. While snags provide optimal denning habitat (Chapter 3), these areas do not provide optimal foraging habitat because of the lack of canopy cover, and dead trees do not provide seeds and cannot support a mycorrhizal community.

MANAGEMENT IMPLICATIONS

Pine, which covers 83% of the Black Hills, was the most important foraging habitat. Future research should concentrate efforts in spruce-dominated habitats, as northern flying squirrels are often associated with spruce (Weigl and Osgood 1974; Mowrey and Zasada 1984; Loeb et al. 2000; Hackett and Pagels 2003; Menzel et al.

2006a, 2006b). The significance of aspen and birch habitat for den sites (Chapter 3) was overshadowed by the dominance of nighttime (foraging) locations in pine habitat.

There is a lack of mycological research for hypogeous fungus and mycophagous small mammals in the Black Hills. Studying hypogeous fungus is difficult due to the lack of ecological information and fluctuations in their seasonal and annual abundance and locations (Fogel 1976; Hunt and Trappe 1987). Vernes (2004) reported low success rate in attempting to dig up truffles in determining composition, distribution, and abundance. I recommend further research collecting small mammal feces to identify fruiting times, composition, distribution, and abundance of fungus throughout the Black Hills. In addition a study of food and den sites as limiting factors for northern flying squirrels would provide a better understanding of resource use and requirements within home ranges.

Table 4-1. Minimum convex polygon (MCP) core areas (50%) and home ranges (100%) by year and sex for northern flying squirrels May-August, 2005-2007 in the Black Hills, South Dakota.

	n	50% MCP (ha) mean \pm SE	100% MCP (ha) mean \pm SE
Southern Hills (2005)			
Males	8	1.74 \pm 0.36	8.58 \pm 1.28
Females	9	1.06 \pm 0.16	4.99 \pm 0.57
All	17	1.38 \pm 0.20	6.68 \pm 0.79
Northern Hills (2006)			
Males	13	3.44 \pm 0.73	15.76 \pm 2.78
Females	5	1.60 \pm 0.21	10.56 \pm 2.63
All	18	2.93 \pm 0.56	14.32 \pm 2.17
Central Hills (2007)			
Males	9	1.83 \pm 0.43	7.03 \pm 1.35
Females	5	1.57 \pm 0.58	6.71 \pm 1.48
All	14	1.74 \pm 0.34	6.91 \pm 0.98
All	49	2.05 \pm 0.25	9.55 \pm 1.01
Males	30	2.50 \pm 0.38	11.23 \pm 1.48*
Females	19	1.34 \pm 0.18	6.91 \pm 0.94*

* Indicates significant difference with Wilcoxon rank sums test ($P \leq 0.05$)

Table 4-2. Continuous variables tested for differences between means of northern flying squirrel tracking locations (1243 points) and hectares available within home ranges (414 ha) during May-August, 2005-2007 in the Black Hills, South Dakota. See methods for description of habitat variables.

Habitat variable	Tracking locations mean \pm SE	Home range mean \pm SE	p-value ^a
Slope (%)	19.19 \pm 0.25	18.11 \pm 0.38	0.23
live trees (#/ha)	1003.27 \pm 30.63	1145.7 \pm 56.46	0.11
live trees >12.7 cm dbh (#/ha)	53.09 \pm 1.10	49.38 \pm 2.00	0.04
live ba (m ² /ha)	27.50 \pm 0.47	25.31 \pm 0.83	0.02
dead ba m ² /ha	7.57 \pm 0.22	8.03 \pm 0.42	0.35
total snags (#/ha)	7.70 \pm 0.27	8.69 \pm 0.46	0.01
down dead (#/ha)	10.55 \pm 0.41	11.93 \pm 0.86	0.67

^a Means tested with Wilcoxon rank sums ($P \leq 0.05$).

Table 4-3. Comparison of minimum convex polygon (MCP) home range sizes for northern flying squirrels across North America.

Study Area	MCP (ha)	Source
Black Hills, SD	9.55 avg (n = 49)	This study
	11.23 male (n = 30)	
	6.91 female (n = 19)	
New Brunswick	12.5 males (n = 7)	Gerrow (1996)
	2.8 females (n = 8)	
NW British Colombia	3.7 males (n = 9)	Cotton and Parker (2000)
	1.4 females (n = 6)	
Virginia	59.8 males (n = 4)	Menzel et al. (2006a)
	15.9 females (n = 8)	
NW British Colombia ^a	10.3 avg (n = 5)	Mahon and Steventon (in litt.)
Western Oregon ^a	4.2 avg (n = 4)	Witt (1992)

^aStudy did not differentiate between males and females.

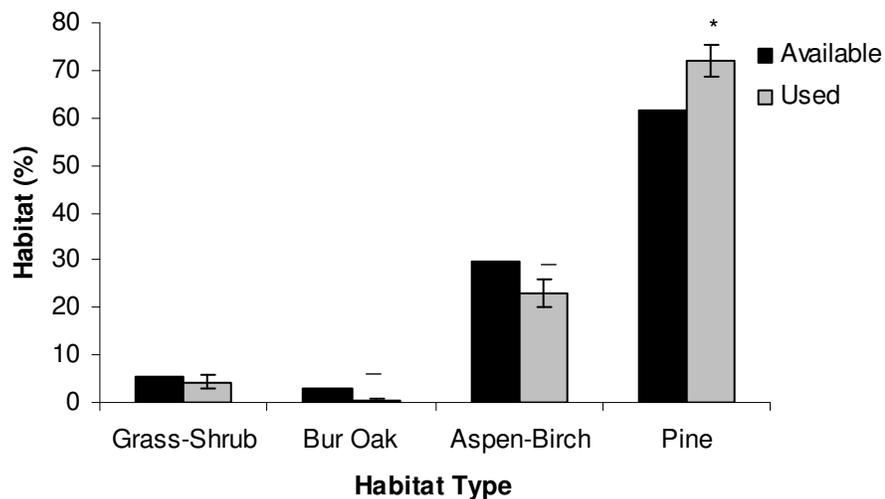


Figure 4-1. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).

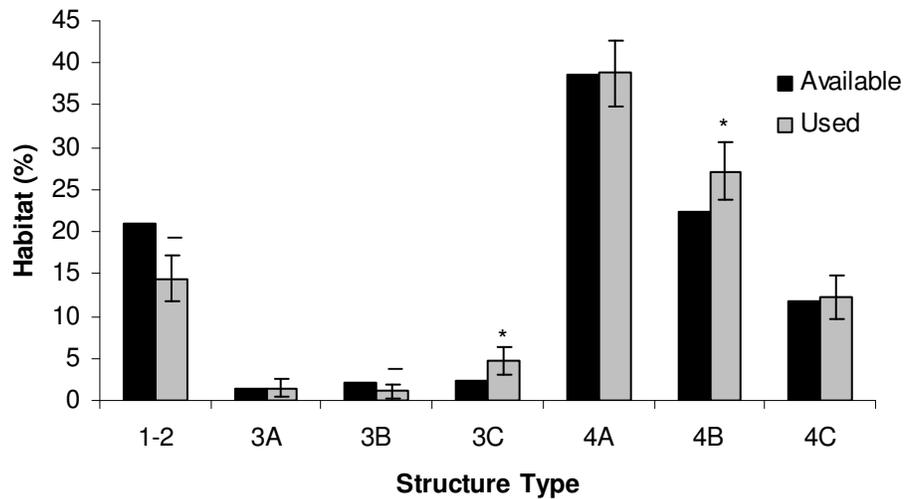


Figure 4-2. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.

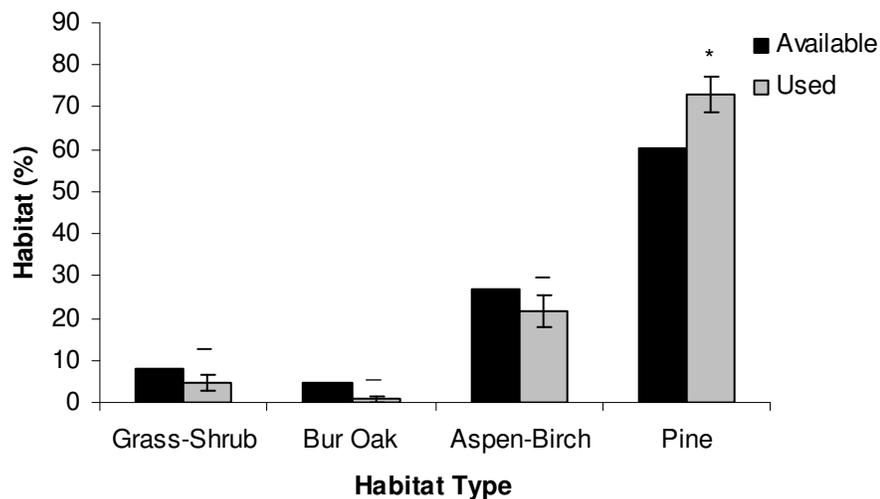


Figure 4-3. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of male northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).

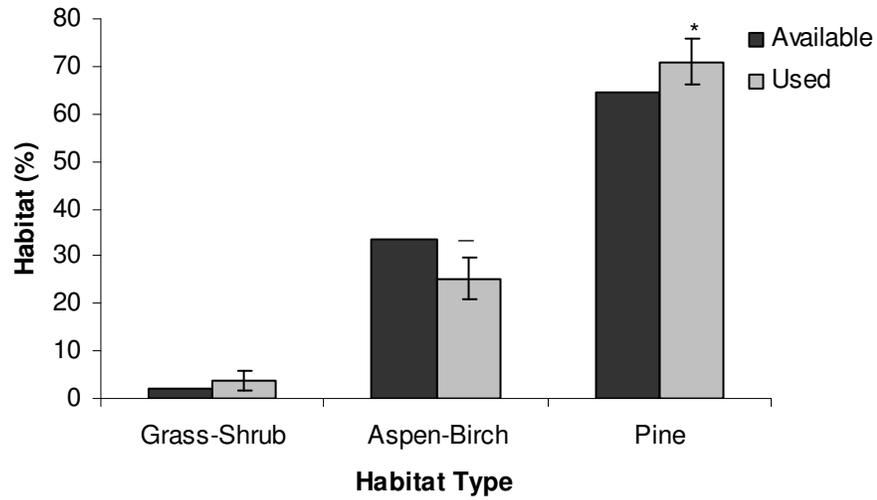


Figure 4-4. Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of female northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$).

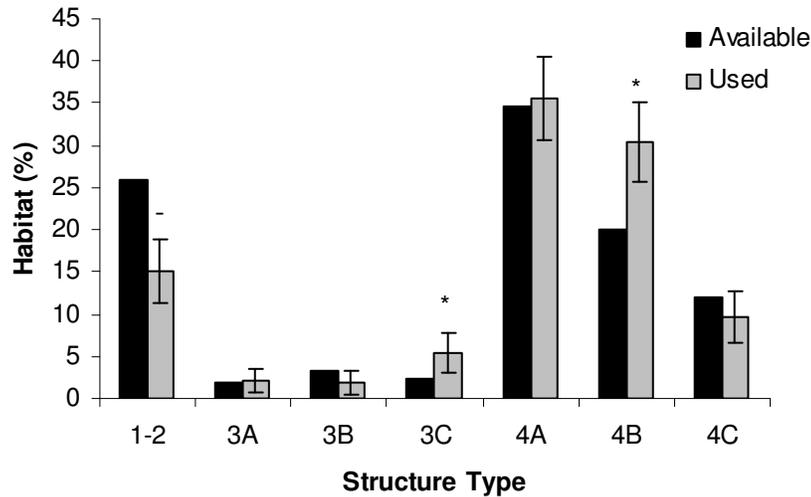


Figure 4-5. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of male northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.

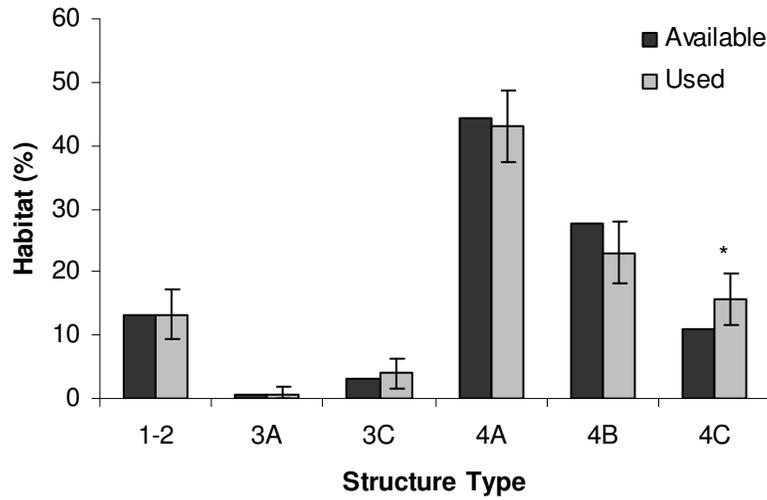


Figure 4-6. Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of female northern flying squirrels with ≥ 10 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Error bars represent Bonferroni confidence interval. Minus (-) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected ($P = 0.05$). Structure type categories: 1-2 = < 2.5 cm dbh; 3A = 2.5-23 cm dbh, 11-40% canopy cover; 3B = 2.5-23 cm dbh, 41-70% canopy cover; 3C = 2.5-23 cm dbh, $> 70\%$ canopy cover; 4A = 23.1-40 cm dbh, 11-40% canopy cover; 4B = 23.1-40 cm dbh, 41-70% canopy cover; and 4C = 23.1-40 cm dbh, $> 70\%$ canopy cover.

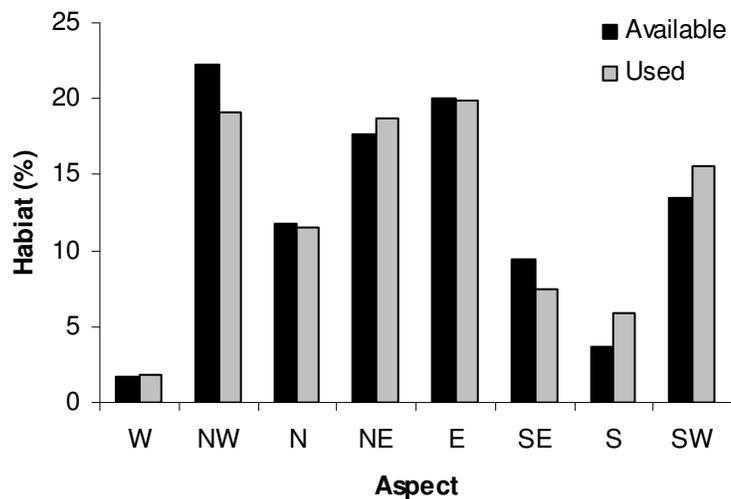


Figure 4-7. Proportion of eight land aspects available within MCP home ranges of northern flying squirrels with ≥ 10 radio-tracking locations and Black Hills study area compared to the proportion of observations (radio-tracking locations) within each aspect May-August, 2005-2007 in the Black Hills, South Dakota.

CHAPTER 5

**RESOURCE SELECTION HABITAT MODEL FOR NORTHERN FLYING
SQUIRRELS IN THE BLACK HILLS, SOUTH DAKOTA**

Abstract: A resource selection function (RSF) habitat model was created for northern flying squirrel distribution throughout the Black Hills. Using methods from Manly et al. (2002) and Johnson et al. (2006), logistic regression was used to compare habitat variables at used locations (observed radio-tracking and trapping locations) to a random sample of available sites throughout the study area [design I resource selection methods (Thomas and Taylor 1990)]. Estimated coefficients of the significant variables from the logistic regression model were incorporated into a GIS raster layer to produce a map with RSF values for the Black Hills. The RSF values were transformed to a relative probability of habitat use ranging from 0 to 1. Independent validation data were used to determine a good model fit based on the predictive performance of the RSF. The RSF map delineates important areas of habitat use by northern flying squirrels throughout the Black Hills and can be used for management purposes, as well as a baseline for future research.

INTRODUCTION

Studying species with low population density, patchy distribution, and a cryptic nature is challenging (Menzel et al. 2006b). Data on macro- and microhabitat research such as habitat use, home range, food habits, etc. are often difficult to gather for these

species. With the advancement of radiotelemetry, animals can be tracked to gain a better understanding of resource requirements. Radio-tracking locations can be integrated into geographic information systems (GIS) to create species-specific resource selection function (RSF) habitat models (Gibson et al. 2004, Posillico et al. 2004). Manly et al. (2002) defined RSFs as any function that is proportional to the probability of use by an organism. Mapping the potential distribution based on model predictions delineates high use areas that aid resource managers in determining important habitats for management (Fielding and Bell 1997).

Based on trapping results (Chapter 2), northern flying squirrels are found throughout the Black Hills, but the density is higher in the northern hills. Even though the northern flying squirrel population seems stable and is widely distributed throughout the Black Hills, identifying areas of high probability of use is important because the population is isolated and forest management decisions can significantly impact the population. The objective of this portion of the study was to create a RSF habitat model for northern flying squirrels in the Black Hills to determine probability of habitat selection throughout the Black Hills. Logistic regression was used to compare habitat variables at radio-tracking and trapping locations (used) to characteristics within the Black Hills study area (available). Logistic regression is commonly used in wildlife studies to predict habitat use throughout a study area (Fielding and Haworth 1995; Mladenoff et al. 1999). Comparing used locations for the population to available locations within the study area is a design I resource selection study (Thomas and Taylor

1990). The GIS map layer produced from the model will help wildlife managers determine important areas for northern flying squirrels.

METHODS

To create a RSF habitat model for northern flying squirrels, I downloaded digital databases from the Black Hills National Forest Service website (USDA Forest Service 2006). The databases included a vegetation polygon layer, digital line graph of streams, and digital elevation model (10-m resolution). Precipitation databases for South Dakota and Wyoming were downloaded from the Water and Climate Center of the Natural Resources Conservation Service website (USDA Natural Resources Conservation Service 2007).

The vegetation layer provided vegetation composition and structure variables along with landscape features for a site. Variables taken from the vegetation layer were habitat types (grass-shrub, aspen-birch, bur oak, pine, and spruce), structural stage (1-2, 3A, 3B, 3C, 4A, 4B, 4C), aspect, # live trees/ha, basal area (m^2) of live trees ≥ 12.7 cm dbh, basal area (m^2) of dead trees ≥ 12.7 cm dbh, # dead and down trees ≥ 12.7 cm dbh, and # snags ≥ 12.7 cm dbh. Spatial analyst extension (Environmental Systems Research Institute 2004) was used in ArcGIS 9.1 to convert the vector polygon layer to a raster dataset with 30-m resolution. Spatial analyst was also used to create a 30-m raster dataset depicting distance from streams. All layers were projected to UTM World Geodetic System 1984 coordinate system. The model was produced for the contiguous national forest land within the Black Hills of South Dakota and Wyoming. JMPIN 4.0 was used

to create the model and the model was integrated into ArcGIS 9.1 to produce the RSF habitat suitability map.

There were 1503 trapping, tracking, and observational locations for northern flying squirrels used in producing and validating the RSF habitat model. The locations were collected from 2005-2007 and data was pooled across all study years. Three hundred (20%) random points were removed from the sample of used locations for use in validating the model. A random sample of 1203 points, with replacement, was taken from the study area to describe the available habitat.

Spatial analyst was used to reclassify categorical variables (aspect, tree species, and structural stage class) into indicator variables, and a separate layer was created for each indicator variable. If the variable was present then the cell was coded '1' and if absent the cell was coded '0'. For example, in the north aspect layer all cells with a north aspect will have a '1' and all other cells will have a '0'. This process was continued for the other seven aspects, as well as dominant tree species and structural stage class.

The used and available point layers for building the model were intersected with variables (Table 5-1) considered for inclusion in the RSF model using the intersect point tool in Hawth's Analysis Tools (Beyer 2007). The resulting attribute tables contained values of each variable at each point. The two attribute tables (used and available locations for model building) were exported to JMPIN and combined. In the table with combined data a column was added and all used points were coded '1', while the available points were coded '0'.

Within the Black Hills, spruce only dominates approximately 2% of the landscape and northern flying squirrel locations from 2005-2007 did not fall within areas dominated by spruce. Therefore, spruce was not considered as a variable in the logistic regression model. However, spruce has been found to be significant in other northern flying squirrel studies across their range (Manville 1949; Connor 1960; Jackson 1961; Musser 1961; Weigl and Osgood 1974; Mowrey and Zasada 1984; Urban 1988; Payne et al. 1989; Loeb et al. 2000; Odom et al. 2001; Hackett and Pagels 2003; Smith and Nichols 2003; Ford et al. 2004; Menzel et al. 2006a), therefore a value of one was added to all cells containing spruce in the RSF model to give weight to spruce habitat.

The model building data were subjected to a series of tests to determine which variables would be incorporated into the final model. Fisher's exact test was used to compare proportions of used and available categorical (indicator) variables. Wilcoxon rank sums test was used to compare means of continuous variables between used (trapping and tracking) locations and available locations (random points throughout the study area). Any categorical or continuous variables found to be significant at the 10% level were retained for further statistical analysis. A correlation matrix was established with retained variables. When two variables were highly correlated ($r \geq 0.70$), the one deemed to be less significant biologically was removed (Manly et al. 2002).

Logistic regression was used to determine coefficients of remaining variables with the dependent variables being used (1) or available (0). Logistic regression has become the standard method of analysis for discrete response outcome variables (Hosmer and Lemeshow 2000), including small mammal studies (Carey et al. 1999; Menzel et al.

2006b). In addition, the assumptions for the independent variables are more lenient and continuous and categorical variables can both be included in the model (Hosmer and Lemeshow 2000). The final RSF model was determined by stepwise backward elimination. In the logistic regression model, likelihood ratio X^2 test was used to determine which variables were significant in determining habitat use by northern flying squirrels at the 10% level (Manly et al. 2002). The variable with the highest likelihood ratio X^2 p-value was removed and logistic regression was run on the remaining variables. This process continued until all variables in the model had a regression coefficient that was significant at the 10% level. The regression coefficients were included in the logistic regression equation

$$w^*(x) = \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_p x_p)$$

where β_0 is the estimated constant intercept coefficient, $\beta_{1..p}$ are the significant regression estimated coefficients, and $x_{1..p}$ are the corresponding variables (Manly et al. 2002).

RSFs in use-availability studies often take on an exponential form of function (Manly et al. 2002; Johnson et al. 2006). Contamination can occur where used locations are included in the sample of available locations. For use-availability studies, the sampling probabilities of used (P_u) and available (P_a) locations are incorporated into the logistic regression model to modify the intercept coefficient (β_0) ($\beta_0 + \log_e[(1-P_a)P_u/P_a]$) (Manly et al. 2002). If the sampling probabilities of used and available locations are not known, then the probabilities along with the constant intercept coefficient are removed from the logistic regression equation, which I did in this study. A RSF is estimated using

the estimated coefficients and significant variables from the logistic regression model with the following formula

$$w(x) = \exp(\beta_1 x_1 + \dots + \beta_p x_p)$$

where $\beta_{1\dots p}$ are significant regression coefficients, and $x_{1\dots p}$ are the corresponding significant variables (Manly et al. 2002). The accepted model was then incorporated into ArcGIS 9.1 to produce a RSF value for each 30-m resolution cell in the study area. The resulting RSF values were used to predict relative probability of selection throughout the study area. RSF values are not an absolute probability, therefore a high probability of use does not define optimal habitat (Manly et al. 2002). The raw RSF scores are transformed to scale the predicted values (w) between 0 and 1 using the following formula

$$\hat{w} = \frac{w(x)}{1 + w(x)}$$

where habitat selection probability increases as the transformed RSF value (\hat{w}) approaches 1. The RSF probabilities from the resulting map were then classified into 10 quantiles which represented ordinal bins (categories) with increasing habitat selection (Johnson et al. 2006).

Statistical methods normally used to test validity of a logistic regression model (ROC, Kappa, and confusion matrix) are not appropriate for use-availability research designs due to contamination (Boyce et al. 2002). The independent validation data were used to validate the model according to methods suggested by Johnson et al. (2006). The utilization $U(x_i)$ value of each of the bins was determined using the formula

$$U(x_i) = w(x_i)A(x_i) / \sum_j w(x_j)A(x_j)$$

where $w(x_i)$ was the midpoint value of the RSF bin (i) and $A(x_i)$ was the area of bin i (Boyce and McDonald 1999). The midpoint value $w(x_i)$ for each bin was the midpoint of the RSF probability range for that bin and the area $A(x_i)$ was total number of pixels for each bin (Johnson et al. 2006). The number of validation observation points within each bin were counted. The expected number of validation observations within each bin (N_i) was estimated using

$$N_i = N * U(x_i)$$

where N was the total number validation points and $U(x_i)$ was the utilization function from above (Johnson et al. 2006). The proportion of expected observations was compared to the proportion of observed validation points using linear regression. The regression line was compared to a slope of zero (use = availability). R^2 was also calculated from the linear regression model comparing proportions of expected and observed points, with a high value indicating an acceptable fit of the model. Spearman rank correlation was conducted between used and observed frequencies to determine degree of correlation. Chi-square goodness-of-fit was calculated and a nonsignificant p-value (≥ 0.05) indicates an acceptable model. Lastly, Pearson χ^2 test was used to determine which bins have an expected value different from observed value.

RESULTS

Locations used by northern flying squirrels were at higher elevations, higher precipitation, closer to streams, had a higher basal area of live trees >12.7 cm dbh and a higher basal area of dead trees >12.7 cm dbh, contained more live trees per hectare, more

dead down trees per hectare, and more snags per hectare than available (Table 5-2). Used locations were comprised of less grass-shrub habitat, more aspen-birch, less structural classes 3A and 3B, and more structural class 4A and 4B than available (Table 5-3). Structural class 4C was marginal ($P = 0.1008$), therefore 4C was considered for the logistic model (Table 5-3). Used locations were also more likely to be on east and northwest slopes, but less likely to be on southeast and west slopes (Table 5-3).

Two variables found to be significant were removed because they were highly correlated ($r \geq 0.70$) with another significant variable. Elevation and precipitation were correlated ($r = 0.75$). Elevation was removed because moisture levels can influence fungus abundance and distribution and therefore, northern flying squirrel abundance and distribution. The variable estimating the number of dead and down trees was correlated with dead basal area ($r = 0.81$). The variable estimating dead and down trees was removed because dead basal area is a measure of standing and down dead trees.

The final estimated RSF was

$$\hat{w} = \exp \{0.0983(\text{Precip}) - 0.0009(\text{DistStrm}) - 0.5634(\text{GRA}) + 1.3875(\text{TAA}) \\ - 2.0695(3A) - 1.8418(3B) - 0.9112(\text{WE}) + 0.3129(\text{NW}) + 0.0005(\text{LiveHa}) \\ + 0.0387(\text{DeadBA}) + 0.0372(\text{TotSnags}) + 1(\text{TWS})\}$$

The final RSF indicated that northern flying squirrels were associated with areas of higher precipitation and closer to streams. Squirrels were associated with aspen-birch habitat, but not grass-shrub habitat (Table 5-4). Structural classes 3A and 3B were used less than available (Table 5-4). Northwest aspect was used more than available, while west was used less than available (Table 5-4). Northern flying squirrels were associated

with a higher density of live trees and snags, as well as a higher basal area of dead trees >12.7 cm dbh (Table 5-4) than available.

The linear regression model comparing the proportion of expected to observed frequencies for each bin indicated a good model fit ($R^2 = 0.85$) (Fig. 5-1). The regression line was significantly different from zero (use \neq availability) ($P = 0.0002$). Spearman rank correlation value was 0.9423 ($P < 0.001$). The goodness of fit X^2 test indicated expected and observed values were significantly different ($X^2 = 48.85$, $df = 9$, $P < 0.0001$). Individual bin Pearson X^2 tests found that five of the ten bins had observed frequencies similar to expected frequencies (Table 5-5). Even though the goodness of fit X^2 test was nonsignificant, all other tests indicate a good model performance between observed and expected frequencies. Therefore, the model was accepted based on validation data. A 30-m resolution map of transformed RSF values ranging from 0-1 probability of habitat selection is depicted in Figure 5-2. The RSF habitat model was compared to a GIS habitat layer for the Black Hills and areas of low, medium, and high probability of use were delineated (Fig. 5-3).

DISCUSSION

Habitat suitability models are an important tool for management of nocturnal and elusive species that are difficult to study. The RSF habitat model for northern flying squirrels in the Black Hills does not give an indication of presence or absence based on habitat characteristics at a site, but instead provides a management tool to identify areas of habitat suitability based on known locations. Trapping results suggest northern flying

squirrels are distributed throughout the Black Hills at varying densities across the landscape. These densities are related to habitat suitability, which is depicted in the habitat model. One caution of RSF habitat models is that maps that predict a high probability of use for certain areas do not define optimal habitat (Manly et al. 2002). However, Rosenberg and Anthony (1992) suggested that because of the distribution of northern flying squirrels throughout their range, this species is highly adaptable and is a habitat generalist. Smith et al. (2004) noted that across northern flying squirrel range there was no single variable or group of variables that explained variation in abundance. Within a region, certain habitats are preferred and may support higher densities of northern flying squirrels. I believe the population of northern flying squirrels in the Black Hills is stable, because I caught northern flying squirrels throughout the Black Hills and found them in less than optimal habitats (edge of harvested and burned areas). Successful breeding and natal production was evident with capturing and observations of juveniles, indicating resources are plentiful.

Northern flying squirrels were positively associated with aspen-birch habitat, but not grass-shrub habitat. Aspen-birch (2% of the landscape) was found to be important denning habitat for northern flying squirrels. Aspen and birch are important for den sites because cavities are readily created by primary cavity users, due to the soft tissue of both tree species (Chapter 3). Aspen and birch do not provide optimal foraging habitats because hypogeous fungi are not associated with these species (Chapter 2). Grass-shrub was not selected because grass and shrubs do not provide optimal denning or foraging sites for northern flying squirrels due to the species' dependence on trees.

Studies in the central Appalachians have found spruce to be the primary predictor in northern flying squirrel presence (Weigl and Osgood 1974; Weigl 1978; Urban 1988; Payne et al. 1989; Loeb et al. 2000; Odom et al. 2001; Hackett and Pagels 2003; Ford et al. 2004; Menzel et al. 2006a, 2006b). Northern flying squirrels are also found in spruce forests across other parts of their range including, southeastern New York (Connor 1960), Great Lakes region (Manville 1949; Jackson 1961), Alaska (Mowrey and Zasada 1984; Smith and Nichols 2003), and Utah (Musser 1961). Across northern flying squirrel distribution range, spruce is an important component of habitat use because they are used for dry nests and spruce provides good protection for the nests due to the density of branches. Also, hypogeous fungi are associated with spruce (Luoma et al. 1991; Loeb et al. 2000; Pyare and Longland 2001). Future research should determine northern flying squirrel abundance in spruce dominated areas of the Black Hills which were inadvertently neglected in this study, due to the small extent of spruce habitat across the landscape.

Northern flying squirrel abundance increases with forest complexity (Weigl et al. 1992; Carey et al. 1999; Carey 2001). The model found that not only was density of live trees important, but so was the basal area of dead trees and total number of snags. Significance in higher density of live trees is a reflection of northern flying squirrel dependence on trees. Live trees provide food sources, such as fungi and seeds, and canopy cover for protection from predators. Habitat features that consistently explain significant variation in northern flying squirrel abundance are forest characteristics associated with snags and down, dead wood or decay (Carey et al. 1999). Cavities in snags provide den sites and fungal diversity has been found to be positively correlated

with the abundance of coarse woody debris (Carey et al. 1999). The highest density of northern flying squirrels occurred in stands with the highest coarse woody debris in Oregon (Carey et al. 1999) and southeastern Alaska (Smith et al. 2004).

Northern flying squirrels in the Black Hills were also positively associated with larger trees, but not canopy cover (structural stages 4A, 4B, and 4C). Large trees serve as den sites and an indication of food availability. Northern flying squirrels select larger trees for day nests (Chapter 3) and larger trees are presumed to indicate a mature stand, which has an established mycorrhizal community and higher density of seed production (Chapter 2).

Northern flying squirrels were positively associated with higher precipitation and closer distances to streams compared to available points throughout the study area. Hypogeous fungi fruiting bodies require moist, nutrient-rich, and cool environments to grow (Pyare and Longland 2001). The northern and central hills provides suitable habitat for fungal production with higher precipitation and a cooler environment than the southern hills. Streams would also provide moister environments and increased fungal production. Northern flying squirrel abundance has been linked to fungus abundance (North et al. 1997; Ransome and Sullivan 1997; Carey et al. 1999; Pyare and Longland 2001) and population distribution may be heterogeneous across landscapes because of the heterogeneous spatial distribution of truffles (Pyare and Longland 2002). An increase in moisture results in an increase in fungal community diversity (Carey and Johnson 1995) and abundance (Luoma et al. 1991).

One problem with the model is the degree of habitat selection in the Black Elk Wilderness Area, which is reserved as a wildlife refuge and timber harvest is restricted. The Black Elk Wilderness area covers about 4,080 ha and is a category 1 management area. The area is managed to protect and perpetuate natural ecological processes with little human interference (USDA Forest Service 1996b). Late successional vegetation occurs in the area. The area consists of a diversity of species composition and structure. I predicted the Black Elk Wilderness area to have a high probability of use because in the Pacific Northwest northern flying squirrel abundance was higher in old-growth and complex young forests than managed coniferous stands (Carey et al. 1992; Witt 1992; Carey 1995; Waters and Zabel 1995). The model suggests that this area is not as highly selected as I would have predicted. I believe three of the habitat variables (number of live trees, dead basal area, and number of snags) found to be significant in the model are not accurate for the Black Elk Wilderness area in the GIS database. All three variables had low values; therefore indicating this area was not suitable as northern flying squirrel habitat. However, during 2005, which had a low trapping success overall, I trapped on the edge of the wilderness area. I captured five adult flying squirrels and four juvenile flying squirrels, indicating that not only are the squirrels in the area, but they are successfully reproducing.

Another problem with the model is the high probability of use for the northern portion of the Jasper burn. The burn area has a high number of snags and therefore a high dead basal area. These high values resulted in a high probability of use for this area.

In other studies, stand replacing fires, such as the Jasper burn, indicated a sink habitat for northern flying squirrels (Chapter 2).

The RSF habitat model is useful to land managers for determining areas and habitat characteristics important to northern flying squirrels. The map shows the predicted spatial distribution of northern flying squirrel habitat (and presumably population) throughout the Black Hills. Future research and surveys will also benefit from the model and map, because northern flying squirrels are secretive and elusive and trapping success is low, therefore the RSF habitat map can be used to determine where to continue research efforts.

Table 5-1. Description of variables considered for the resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota.

Variable	Description
Continuous	
Elev	Elevation in meters.
Precip	Average annual precipitation in centimeters.
DistStrm	Distance to nearest stream in meters.
LiveHa	Total number of live trees per hectare.
LiveBA	Basal area (m ² /ha) of live trees ≥ 12.7 cm dbh.
DeadBA	Basal area (m ² /ha) of dead trees ≥ 12.7 cm dbh. This includes all standing mortality, down mortality, standing sound snags, down sound snags, or standing unsound snags.
DeadDown	The number of dead and down trees with a dbh ≥ 12.7 cm. This includes down mortality, down sound snags, or down unsound snags.
TotalSnags	Total number of standing mortality trees, hard snags, and soft snags with a dbh >12.7 cm per hectare.
Categorical	
GRA	Grass-shrub habitat
TAA	Aspen-birch habitat
TBO	Bur oak habitat
TPP	Ponderosa pine habitat
3A	Habitat structural stage with trees 2-23 cm dbh and 11–40% canopy cover.
3B	Habitat structural stage with trees 2-23 cm dbh and 41–70% canopy cover.
3C	Habitat structural stage with trees 2-23 cm dbh and $<71\%$ canopy cover.
4A	Habitat structural stage with trees 23-40 cm dbh and 11-40% canopy cover.
4B	Habitat structural stage with trees 23-40 cm dbh and 41-70% canopy cover.
4C	Habitat structural stage with trees 23-40 cm dbh and $<71\%$ canopy cover.
NO	North aspect
NE	Northeast aspect
EA	East aspect
SE	Southeast aspect
SO	South aspect
SW	Southwest aspect
WE	West aspect
NW	Northwest aspect

Table 5-2. Chi-square tests comparing means of tracking locations (used) (n = 1203) and random locations throughout the study area (available) (n = 1203) to determine continuous variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.

Variable	Used	Available	Z	P-value ^a
	mean \pm SE	mean \pm SE		
Elev ^b	1755.11 \pm 5.89	1669.74 \pm 7.07	8.14	0.0000
Precip	25.14 \pm 0.09	23.58 \pm 0.14	10.36	0.0000
DistStrm	269.14 \pm 7.03	292.34 \pm 7.30	-3.36	0.008
LiveHa	1048.89 \pm 33.70	471.50 \pm 20.49	15.87	0.0000
LiveBA	28.57 \pm 0.47	24.64 \pm 0.58	5.81	<0.0001
DeadBA	7.22 \pm 0.22	4.07 \pm 0.20	16.21	0.0000
DeadDown ^b	9.97 \pm 0.41	5.93 \pm 0.42	8.94	0.0000
TotalSnags	7.46 \pm 0.26	3.36 \pm 0.19	15.99	0.0000

^a Means tested with Wilcoxon rank sums ($P \leq 0.10$)

^b Removed due to correlation ($r \geq 0.70$).

Table 5-3. Fisher's exact test comparing proportion of tracking locations (used) (n = 1203) and random locations throughout the study area (available) (n = 1203) to determine categorical variables retained for resource selection function (RSF) habitat model of northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.

Variable	Used (%)	Available (%)	P-value ^a
GRA	4.82	22.36	<0.0001
TAA	12.14	2.58	<0.0001
TBO	0.17	0.25	1.0000
TPP	82.88	72.74	<0.0001
3A	1.16	4.82	<0.0001
3B	1.16	6.98	<0.0001
3C	4.16	3.41	0.3927
4A	36.41	28.01	<0.0001
4B	30.67	23.69	0.0001
4C	12.97	10.72	0.1008
NO	10.81	9.39	0.2790
NE	18.12	16.63	0.3603
EA	17.87	14.63	0.0356
SE	8.06	10.31	0.0663
SO	6.65	8.40	0.1219
SW	16.87	19.29	0.1379
WE	3.24	12.64	<0.0001
NW	18.37	8.73	<0.0001

^a Means tested with Fisher's exact test ($P \leq 0.10$).

Table 5-4. Estimated coefficients for the resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota. See table 5-1 for description of variables.

Coefficient	Estimate	<i>SE</i>	X^2	P-value ^a	Odds ratio
Precip	0.0983	<i>0.0129</i>	59.80	<0.0001	1.10
DistStrm	-0.0009	<i>0.0002</i>	17.13	<0.0001	1.00
GRA	-0.5634	<i>0.0838</i>	50.27	<0.0001	0.32
TAA	1.3875	<i>0.1642</i>	118.03	<0.0001	16.04
3A	-2.0695	<i>0.2657</i>	88.28	<0.0001	0.02
3B	-1.8418	<i>0.2421</i>	97.70	<0.0001	0.03
NW	0.3129	<i>0.0741</i>	18.48	<0.0001	1.87
WE	-0.9112	<i>0.1118</i>	81.55	<0.0001	0.16
LiveHa	0.0005	<i>0.0001</i>	93.72	<0.0001	1.00
DeadBA	0.0387	<i>0.0097</i>	16.77	<0.0001	1.04
TotSnags	0.0372	<i>0.0086</i>	20.98	<0.0001	1.04

^a Coefficients tested with likelihood ratio X^2 ($P \leq 0.10$).

Table 5-5. Comparison of observed and expected frequencies for resource selection function (RSF) probability values categorized into 10 quantile bins to determine validity of RSF model. RSF values are probability of selection by northern flying squirrels in Black Hills, South Dakota based on trapping and tracking results May-August, 2005-2007.

RSF Bin	Bin range	Bin midpoint $w(x_i)$	# pixels $A(x_i)$	Observed		Expected		p-value ^a
				N	%	n	%	
1	0.044 - 0.690	0.367	512895	0	0.00	3	0.99	0.08
2	0.690 - 0.795	0.743	510101	5	1.67	9	2.95	0.29
3	0.795 - 0.866	0.831	525449	11	3.67	15	5.06	0.43
4	0.866 - 0.903	0.885	507894	4	1.33	21	6.84	0.00
5	0.903 - 0.933	0.918	541661	12	4.00	28	9.38	0.01
6	0.933 - 0.955	0.944	505975	14	4.67	32	10.71	0.01
7	0.955 - 0.974	0.965	544236	45	15.00	41	13.62	0.67
8	0.974 - 0.985	0.980	467932	33	11.00	41	13.51	0.35
9	0.985 - 0.993	0.989	401043	63	21.00	39	13.12	0.02
10	0.993 - 1.000	0.997	651218	113	37.67	71	23.82	0.00

^a Observed versus expected frequencies tested with Pearson X^2 ($P \leq 0.05$).

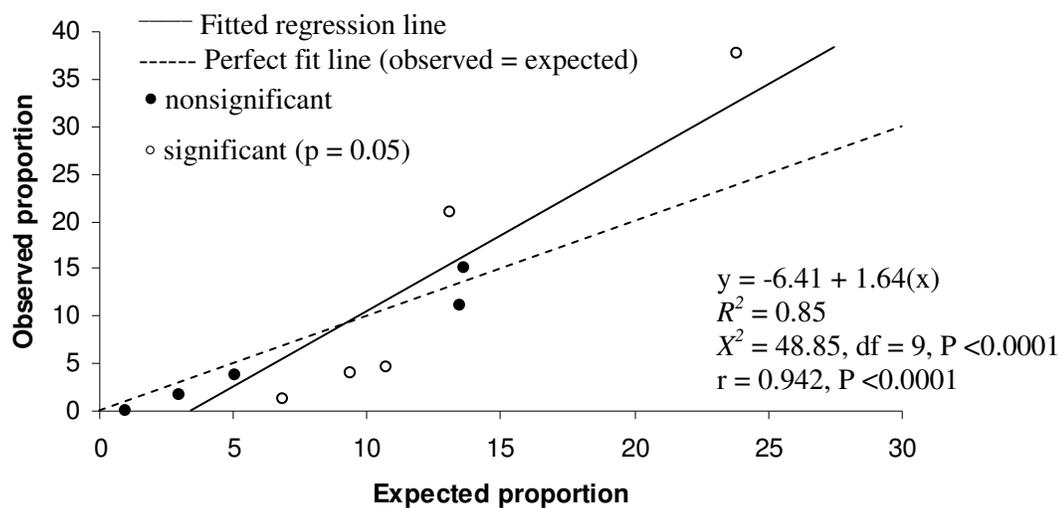


Figure 5-1. Fitted regression of 10 resource selection function bins for proportion of expected versus observed validating data locations ($n = 300$) for resource selection function (RSF) habitat model for northern flying squirrels studied May-August, 2005-2007 in the Black Hills, South Dakota.

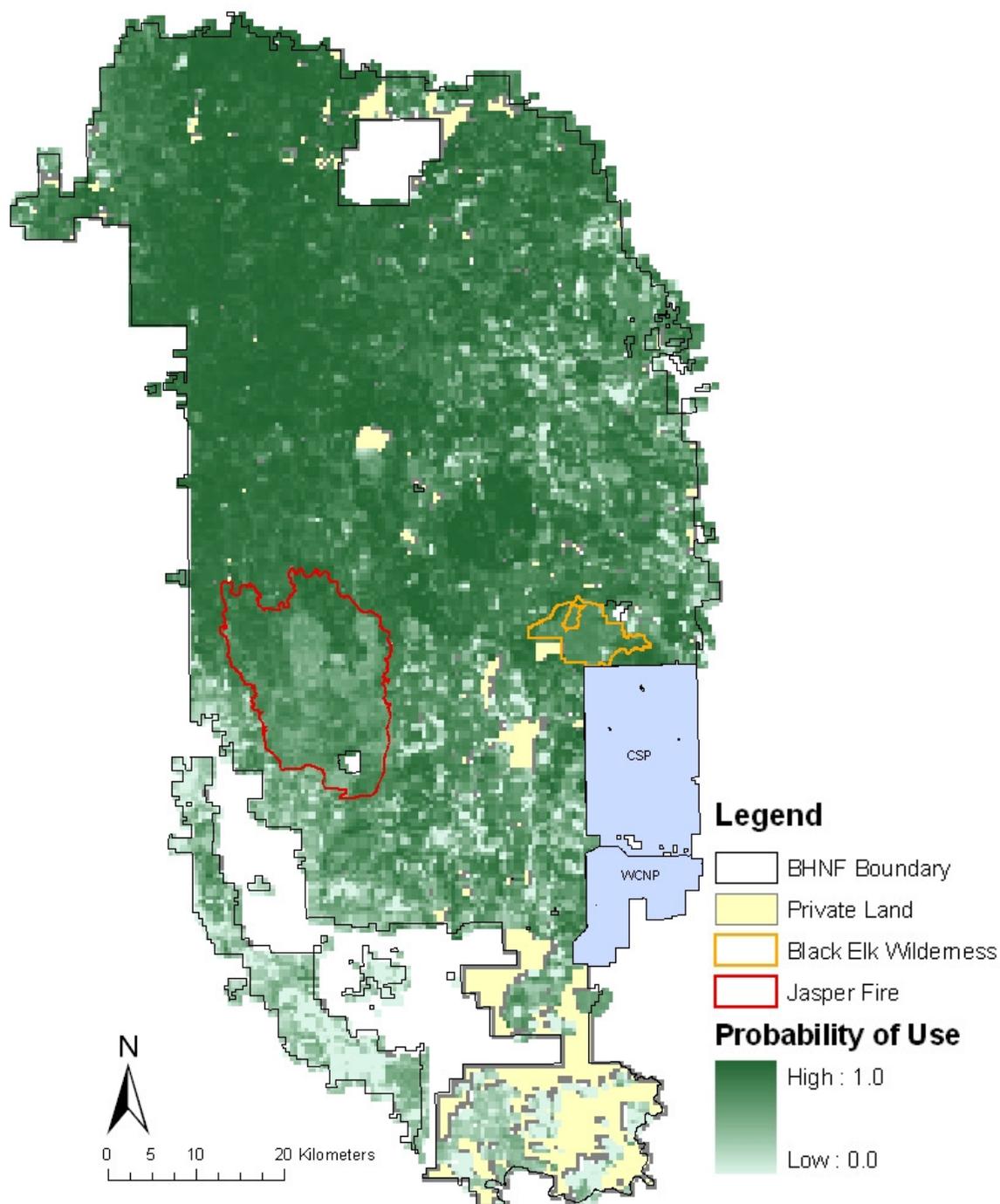


Figure 5-2. Map depicting relative probability of habitat use (30-m) by northern flying squirrels May-August, 2005-2007 throughout the Black Hills, South Dakota.

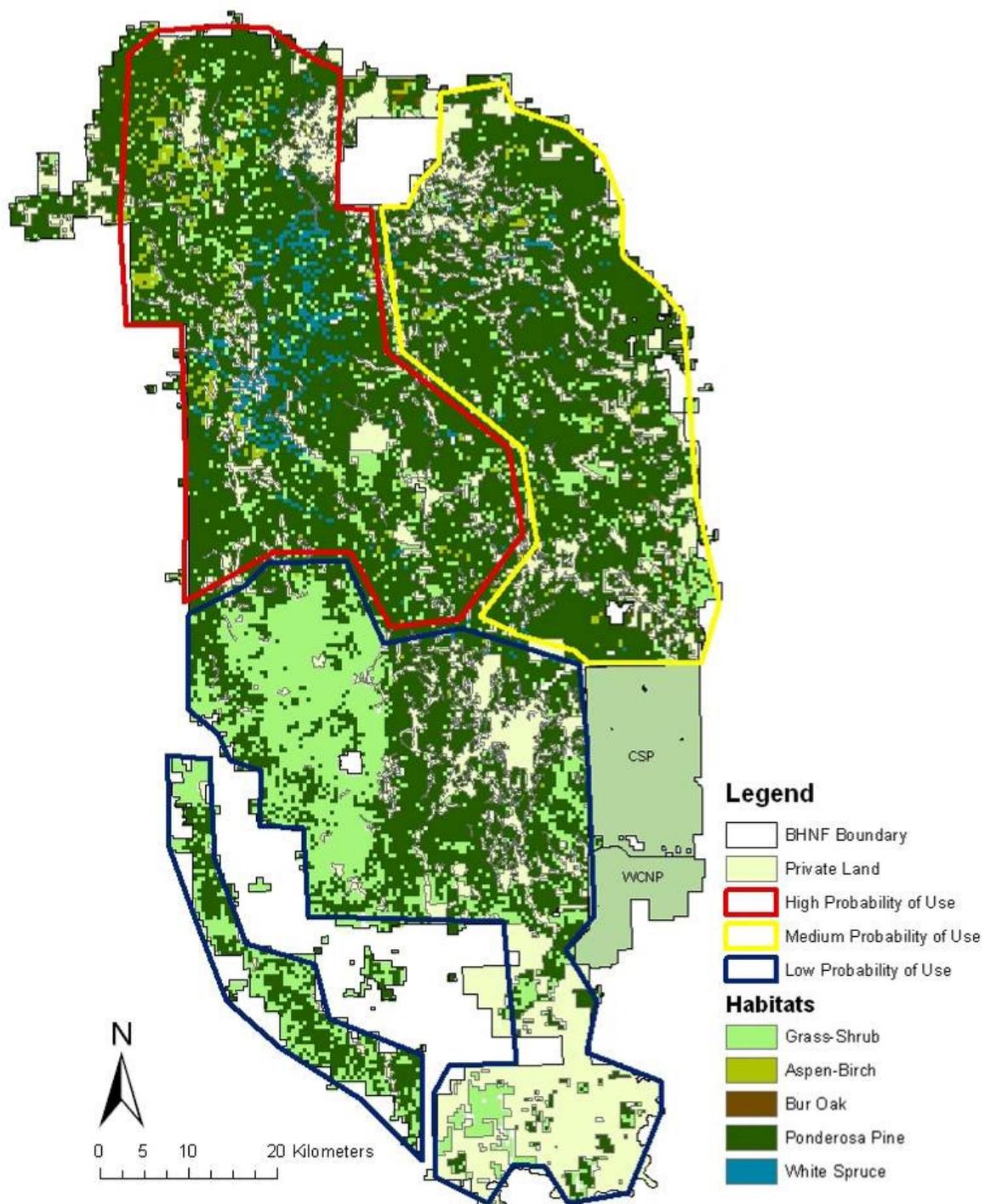


Figure 5-3. Map depicting high, medium, and low probability of habitat use based on resource selection function habitat model (Fig. 5-2) and dominant habitat throughout the Black Hills, South Dakota for northern flying squirrels May-August, 2005-2007.

CHAPTER 6 CONCLUSIONS

Northern flying squirrels and red squirrels were found throughout the Black Hills at varying densities depending on habitat characteristics. Based on trapping results, northern flying squirrel density was highest in the northern and central Black Hills, while red squirrels density was highest in central and southern Black Hills. Both squirrel species were captured on the edge of burns and timber harvests, which other studies have found to be sink habitats (Fisher and Wilkinson 2005).

This study supports northern flying squirrels as habitat generalists, as has been suggested by other studies (Rosenberg and Anthony 1992). Radio-tracking and trapping data were incorporated into a RSF model to determine optimal habitat for northern flying squirrels in the Black Hills. Based on the model and information gathered from other literature, optimal habitat is mature mixed forest with diversity in vegetation composition and structure. Aspen and birch trees are important to provide cavities for denning. Live aspen and birch have several advantages over snags, including a stable structure that persists longer and overhead canopy cover. Spruce and pine are important habitats, providing food resources, such as seeds and hypogeous fungi (Loeb et al. 2000), as well as stable structures for dray nests.

Pine has increased over the last century due to silviculture management for timber production and fire suppression. By placing less emphasis on management for timber production and allowing natural disturbances to take place, the forest can return to conditions suitable for tree-dependent species isolated to the region such as northern flying squirrels. Periodic thinning by mountain pine beetle provides snags and down

woody debris, and opens up the canopy allowing regeneration (Shepperd and Battaglia 2002). Low intensity ground fires provide a mosaic of conditions, including openings, areas of seedlings and smaller trees, and areas of larger trees. With low intensity fires, seed sources are left for recolonization of the site and conditions provided by the fire are favorable for recolonization, rather than sterilization which can be caused by high intensity fires. The amount of aspen and birch habitat can be increased by removing pine. Aspen and birch are early seral shade intolerant trees and pine is shade tolerant and competes for resources required by aspen and birch (Shepperd and Battaglia 2002). Removing pine creates open areas, which encourages aspen and birch to occupy. Spruce habitat can also be increased by removing pine. Spruce is the most shade tolerant species in the Black Hills (Shepperd and Battaglia 2002). Once spruce saplings have established, pine should be removed from areas where pine and spruce coexist or where spruce has been outcompeted by pine to allow opportunity for the spruce to grow.

Northern flying squirrels can exist in a forest mosaic that results from naturally occurring patchy landscapes from disturbances such as fire, windblow, and insect outbreaks. While northern flying squirrels are able to exist in monocultures due to their adaptability, monocultures are not optimal habitat. Mature stands where succession and disturbance are allowed to take place naturally, allow for understory and seral species, because openings are created (Shepperd and Battaglia 2002). Uresk and Severson (1989) suggested diversity would be greatest with management of all stocking levels, including clearcuts and unthinned dense stands, and stocking levels were distributed across the landscape to maximize benefit to wildlife.

Mature forests are important for providing large trees for denning, higher seed production, and mature mycorrhizal fungal communities. Mature forests also provide ground and canopy cover protection while northern flying squirrels forage on the ground. Diversity in structure can be increased by allowing understory components, snags, as well as down woody debris. Understory is important for protection from aerial predators as well as providing additional hosts for mycorrhizal fungi. Dead trees, including standing and down snags, are important as well. Snags provide cavities for den sites and down snags provide a substrate for fungal growth. When timber harvesting, the retention of residual trees is important for future snag retention and maintaining the mycorrhizal fungus community. Residual trees provide seeds necessary to regenerate the disturbed area and a corridor for tree-dependent species to disperse between more suitable habitats. Down woody debris adds to the structural complexity of the forest. Coarse woody debris has the potential to hold large amounts of water that is important to the development of fungi (Hassinger 1989). Ground debris left after a logging operation should be retained as coarse woody debris (Shepperd and Battaglia 2002).

This study provided baseline information on a wide range of topics concerning red squirrel research techniques and distribution, as well as northern flying squirrel research techniques, ecology, and habitat use within the Black Hills. Future research should concentrate on expanding knowledge on both populations in the hills to better understand microhabitat requirements, differences in habitat use between north, central, and southern hills, and limiting factors. Further research should assess reproductive rates, survival, and fitness throughout the Black Hills to better understand habitat deemed

to be optimal, as well as response of both squirrel species to large area disturbance, such as timber harvests and burns.

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Appendix 4-1. Minimum convex polygon core areas (50% MCP) and home ranges (100% MCP) of radio-tracked northern flying squirrels with ≥ 15 radio-tracking locations May-August, 2005-2007 in the Black Hills, South Dakota. Number of radio-tracking locations used to generate home range estimates is "n".

ID	Year	Sex	n	50% MCP (ha)	100% MCP (ha)
10205 ^a	2005	F	13	0.33	1.02
14005	2005	F	32	1.58	6.65
65305	2005	F	29	1.42	4.23
68205	2005	F	32	1.48	4.01
69005	2005	F	28	1.37	7.16
83205	2005	F	30	1.25	7.45
84405	2005	F	30	0.19	4.57
85205	2005	F	16	0.53	3.65
87605	2005	F	27	0.89	2.51
892105 ^a	2005	F	10	0.14	0.57
892205	2005	F	29	0.83	4.73
17205	2005	M	29	1.58	14.18
22105	2005	M	30	0.93	7.91
23205	2005	M	16	1.12	4.45
61105	2005	M	34	0.83	3.86
81205	2005	M	30	2.17	12.09
86405	2005	M	30	1.97	8.39
90305	2005	M	28	3.98	10.81
97205	2005	M	30	1.35	6.96
10306	2006	F	22	1.43	13.71
190106	2006	F	23	1.11	6.36
182206	2006	F	19	2.39	12.73
1143106 ^a	2006	F	12	0.32	1.75
1143206	2006	F	24	1.64	19.97
114006	2006	F	28	1.45	6.71
1691206 ^a	2006	F	11	2.28	6.38
10106	2006	M	27	2.44	14.46
186206	2006	M	21	8.04	35.63
184206	2006	M	20	0.98	23.69
182306	2006	M	25	2.97	9.54
181106	2006	M	20	5.44	19.35
168306	2006	M	25	3.53	12.96
122206	2006	M	26	1.76	5.92
117106	2006	M	22	1.26	8.47
852206	2006	M	23	2.56	13.43
89206	2006	M	22	0.93	11.35
97206	2006	M	18	8.63	37.41
61206	2006	M	22	5.06	16.76
65306 ^a	2006	F	11	0.32	1.23
187206	2006	M	24	1.05	5.65
85207	2007	F	21	0.55	2.98
97207	2007	F	23	3.37	8.63

Appendix 4-1. Continued

117107	2007	F	21	0.83	10.77
122207	2007	F	21	2.56	7.49
1822607	2007	F	21	0.56	3.68
61207	2007	M	21	0.85	5.35
1142607	2007	M	21	1.28	6.14
1142707	2007	M	21	3.33	15.91
168307	2007	M	24	4.56	10.51
169307	2007	M	20	2.12	7.85
1822907	2007	M	19	1.42	6.03
184107	2007	M	22	1.06	3.38
184207	2007	M	20	0.76	2.66
190207	2007	M	20	1.11	5.40
117107	2007	F	21	0.83	10.77
122207	2007	F	21	2.56	7.49
1822607	2007	F	21	0.56	3.68
61207	2007	M	21	0.85	5.35
1142607	2007	M	21	1.28	6.14
1142707	2007	M	21	3.33	15.91

^a Radio-collared squirrels used in habitat use analysis ($n \geq 10$), but eliminated for home range analysis ($n < 15$).