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Home Range and Habitat Use of Northern Flying Squirrels in the Black Hills, South Dakota

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ABSTRACT.—Northern flying squirrels (*Glaucomys sabrinus*) of the Black Hills National Forest (BHNF) of South Dakota represent a unique and isolated population, but little is known about the home range size and habitat use of this population. Fifty-nine northern flying squirrels (34 males and 25 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 $\geq$15 radio-tracking locations (n = 49). Males occupied larger home ranges (n = 30; 11.23 $\pm$ 1.48 ha) than females (n = 19; 6.91 $\pm$ 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 $\geq$10 radio-tracking locations (n = 54). Habitat 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). Ponderosa pine (*Pinus ponderosa*), which dominates 83% of BHNF, was the only habitat used proportionally more than available. Within their home ranges northern flying squirrels also selected larger trees and more canopy cover, as well as more live trees >12.7 cm dbh, higher basal area of live trees and fewer snags. This study aids managers in understanding habitat use by northern flying squirrels in pine dominated habitat of BHNF and an isolated population at the southern edge of their range.

INTRODUCTION

Home range was first defined by Burt (1943) as the area regularly used by an individual animal that includes all resources necessary for daily survival. One method of determining home range size is minimum convex polygon (MCP) home ranges, which are determined by connecting the peripheral radio-tracking points for each animal (Mohr, 1947). Habitat selection or avoidance within home ranges 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 (Neu *et al.*, 1974). When resources are used more than expected based on availability, there is a selection 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).

In the Black Hills National Forest (BHNF), there is an isolated population of northern flying squirrel, *Glaucomys sabrinus bangsi* (Rhoads) (King, 1951; Wells-Gosling and Heaney, 1984) that is restricted to this region of western South Dakota. Due to its rarity, isolation and population risk northern flying squirrels within the BHNF are considered a Forest Service Species of Local Concern (USDA Forest Service, 2005) and a Species of Special Concern (S2) by the South Dakota Natural Heritage Program (South Dakota Department of Game Fish and Parks, 2006). With the lack of information for northern flying squirrels in BHNF,

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their role in the ecosystem is not well understood. However, across their range northern flying squirrels are mycophagous and play an important role in dispersing mycorrhizal fungal spores (Maser *et al.*, 1978; North *et al.*, 1997; Ransome and Sullivan, 1997; Carey *et al.*, 1999; Loeb *et al.*, 2000; Pyare and Longland, 2001; Vernes *et al.*, 2004), making the squirrels part of a squirrel-fungus-tree mutualism that may help maintain the forests (Weigl, 2007). During our study we observed northern flying squirrels consuming hypogeous fungus and Gabel *et al.* (2006) found that 90% of the contents of northern flying squirrel feces collected from captured squirrels in the northern BHNF were fungal spores.

Northern flying squirrels home range size may be influenced by availability of suitable den sites (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). In the BHNF, northern flying squirrels are associated with cavities in live quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) trees and aspen, birch and ponderosa pine (*Pinus ponderosa*) snags, as well as drays nests in large live ponderosa pine and Black Hills white spruce (*Picea glauca*) trees (Hough, 2008). Northern flying squirrel diet primarily consists of mycorrhizal fungus fruiting bodies, truffles, (North *et al.*, 1997; Carey *et al.*, 1999; Ransome and Sullivan, 1997, 2004; Weigl, 2007), but they also consume lichens, buds, berries, staminate cones and animal material (Weigl, 2007). Movements, home range size and use of space appear to be influenced mostly by availability of food resources (Menzel *et al.*, 2006a), primarily the distribution of truffles (Gomez, 2005).

Despite the increase in northern flying squirrel research the last two decades across their range, disjunct populations at the southern edge of their range, such as the BHNF population, have not been well studied (Weigl, 2007). Prior to this study two other studies were conducted in (northern BHNF; Krueger, 2004) or adjacent to (Wind Cave National Park; Duckwitz, 2001) BHNF, but they were limited in study area extent and duration. Currently no data exist on den habitat use of northern flying squirrels in the BHNF and across their range within forest stands dominated by ponderosa pine and intensively managed for timber. Studying the BHNF population is important because there is a threat to disjunct squirrel populations, such as those at the southern edge of their range, which may be impacted by human activities, such as clear-cutting, development or anything destroying extensive tracts of habitat (Koprowski, 2005; Weigl, 2007). Smith (2007) also suggested priority for researching northern flying squirrels be on the edge of the geographic distribution where knowledge is scarce.

We evaluated home range size for northern flying squirrels and assessed habitat selection within home ranges. We evaluated home range sizes between males and females and habitat use by sex (to evaluate differences in resource use between sexes), because the squirrels were tracked during the time females were pregnant and/or rearing young. This information will assist managers in the BHNF by providing information on microhabitat resource use and also contribute to the limited knowledge of northern flying squirrel habitat use within an isolated portion of the flying squirrel's southern range.

MATERIALS AND METHODS

Study area.—This study was conducted in the BHNF, located in western South Dakota (UTM 13N 574719–641489 E, 4809979–4932866 N) (Fig. 1). The BHNF is a unique ecosystem that consists of forest surrounded by Great Plains grasslands (Froiland, 1990). The ponderosa pine dominated hills extend 900–1200 m above the surrounding Great Plains prairie. The Black Hills were formed by mountain uplift, extend 200 km north to south and 100 km east to west and encompass 486,000 ha. Their elevation range is

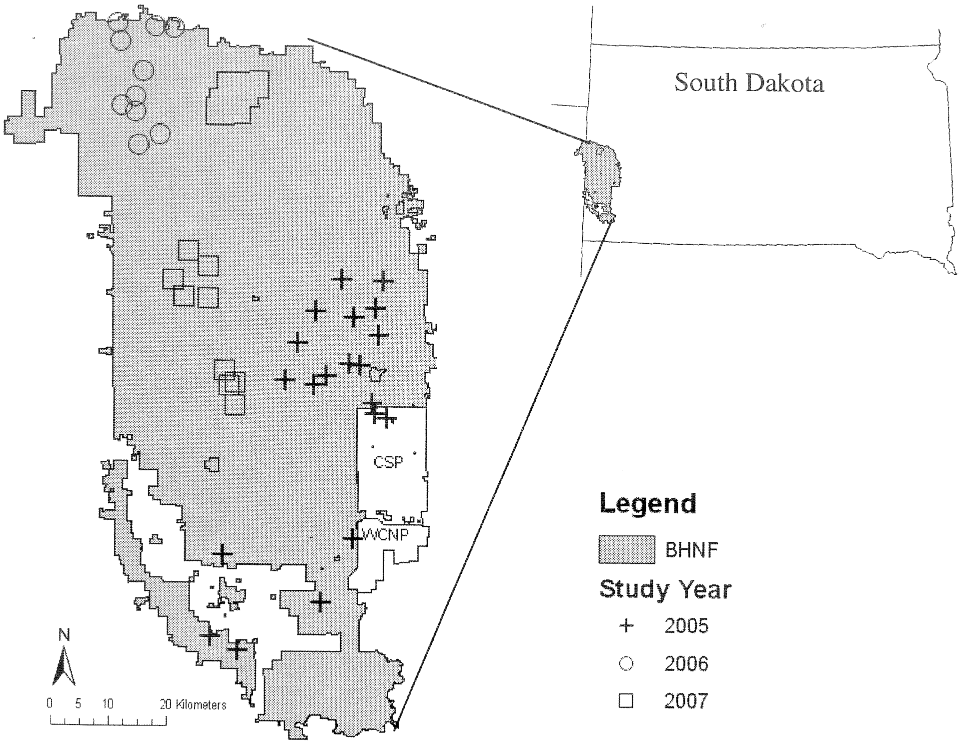

FIG. 1.—Location of trap sites for northern flying squirrels in the Black Hills National Forest (BHNF) (May through Aug. 2005–2007). Custer State Park (CSP) and Wind Cave National Park (WCNP) are located in the southeast portion of the Black Hills region

approximately 1200 to 2207 m, with the forested region extending to 2102 m (Froiland, 1990).

The southern Black Hills, has a warmer (9.3 C) and drier (45–51 cm/y) annual climate than the northern portion of the range (7.2 C and 61–66 cm/y; Shepperd and Battaglia, 2002). Ponderosa pine is found throughout the BHNF and is the most abundant tree species, dominating 83% of the landscape (USDA Forest Service, 2005). In the central to southern hills quaking aspen and paper birch are interspersed with pine in the bottomlands and along water sources, spruce occurs sporadically and is commonly found along streams, and there is little to no understory. In the northern hills white spruce is more abundant, comprising 2% of the vegetation (USDA Forest Service, 2005). The northern hills has an understory component, primarily bur oak (*Quercus macrocarpa*), but may also include American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*) and eastern hop-horn-beam (*Ostrya virginiana*) (Hoffman and Alexander, 1987). Quaking aspen and paper birch dominate moister environments, particularly in disturbed areas, of the central to northern BHNF (Hoffman and Alexander, 1987).

Trapping and radio-tracking.—May through Aug. 2005, we trapped northern flying squirrels along established transects throughout the southeastern BHNF. Ten Tomahawk live traps (Model 201: 40 × 13 × 13 cm, Tomahawk Live Trap Co., Tomahawk, WI.) were placed 50 m apart; this distance ensures at least four traps were in each northern flying squirrel's home range (Hough, 2008) and accounts for home range overlap between squirrels (Carey *et al.*, 1991). Trap placement was alternated between the ground at the base of a tree and on a branch of a tree, secured at a 1 to 2 m height. We covered traps with ground litter and bark and baited each with oil-packed tuna or a mixture of peanut butter, oatmeal and bacon grease. Two different types of baits were used for a related study comparing bait selection.

May through Aug. 2006 and 2007, we trapped northern flying squirrels along established transects throughout the northern BHNF and western BHNF, respectively. We placed all traps in trees, because capture success of tree traps was greater than ground traps during 2005. We alternated 10 single-door Tomahawk live traps and 10 double-door Havahart live traps (Model 1025: 45.7 × 12.7 × 12.7 cm, Woodstream Corporation, Lititz, PA). All traps were baited with a mixture of peanut butter, oatmeal and bacon grease. During all years, we set traps for at least 14 trap nights and checked them each morning.

Fifty-nine northern flying squirrels (>100 g; 8 males and 12 females in 2005, 17 males and 8 females in 2006 and 9 males and 5 females in 2007) were anesthetized with halothane and fitted with ATS model M1610 radio transmitter collars (Advanced Telemetry Systems, Isanti, MN). Collars weighed 4.0 grams, approximately 2.1% to 3.5% of the northern flying squirrel's body weight. We released captured northern flying squirrels when they were fully recovered from our administered anesthetic.

Radio-tracking.—We located radio-collared northern flying squirrels with a Yagi antenna and model R2000 ATS receiver. To determine home range size radio-tracking was conducted during the squirrel's active period (8 p.m. to 5 a.m.) by point sampling (Kenward, 2001) by foot. We could not use triangulation, because the radio-transmitters only had a range of about 800 m, and steep ridges significantly decreased the range (400 m), especially in the northern hills. Every 2 to 4 wk radio-collared northern flying squirrels were tracked during the day to monitor den use and these points were also included in the home range estimate. For each squirrel, points were collected at least 3 h apart to avoid autocorrelation. All locations were recorded with a Garmin eTrex Vista GPS (Garmin International Inc., Olathe, KS) in Universal Transverse Mercator (UTM) coordinates. All methods were approved by South Dakota State University Institutional Animal Care and Use Committee.

Home range.—We used the Home Range Extension (Rodgers *et al.*, 2007) in ArcGIS 9.1 to calculate 100% minimum convex polygon (MCP) home ranges for all northern flying squirrels with ≥15 radio-tracking points. Wilcoxon rank sums test was used to examine home range sizes between sex. Kruskal-Wallis test was used to examine home range sizes between years.

Habitat use.—To determine habitat selection within home ranges, we 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. Neu *et al.* (1974) methods were used for all nominal variables. First, we used likelihood ratio χ^2 test to examine differences between frequency of available (number of hectares) habitat within home ranges to the frequency of observed locations (number of telemetry points) in each habitat. When likelihood ratio χ^2 indicated significant differences between use and availability, we identified which habitat types were selected or avoided, by calculating Bonferroni z-statistic confidence intervals for proportional use estimates for each habitat and structural class. The χ^2 test was used for habitat selection within home ranges on all radio-collared squirrels and also by sex, to determine if males and females selected similar habitats. Continuous variables were tested with Wilcoxon rank sums test to determine if there was a difference between the means of radio-tracking locations and available hectares within home ranges.

TABLE 1.—Minimum convex polygon (MCP) home ranges by year and sex for northern flying squirrels in the Black Hills National Forest (May through Aug. 2005–2007)

	n	100% MCP (ha) mean ± SE
Southern Hills (2005)		
Males	8	8.58 ± *1.28*
Females	9	4.99 ± *0.57*
All	17	6.68 ± *0.79*
Northern Hills (2006)		
Males	13	15.76 ± *2.78*
Females	5	10.56 ± *2.63*
All	18	14.32 ± *2.17*
Central Hills (2007)		
Males	9	7.03 ± *1.35*
Females	5	6.71 ± *1.48*
All	14	6.91 ± *0.98*
All	**49**	**9.55 ± *1.01***
Males	**30**	**11.23 ± *1.48****
Females	**19**	**6.91 ± *0.94****

* Indicates significant difference with Wilcoxon rank sums test (P ≤ 0.05)

The nominal variables are habitat, structural class and aspect. There were four habitat types, pine, aspen-birch, bur oak and grass-shrubs. The USFS has established structural classes based on canopy cover and dbh for BHNF (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%. The structural classes are 1–2, 3A, 3B, 3C, 4A, 4B, 4C and 5. The aspect classes were north, northeast, east, southeast, south, southwest, west and northwest. Continuous variables are 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.

Statistical analyses were conducted using JMP IN 4.0 (SAS Institute Inc., Cary, North Carolina) using an $\alpha = 0.05$. Shapiro-Wilk's test was used to test all variables for normality. Because assumptions of normality and heterogeneity were not always met we performed nonparametric tests. We felt data met requirements for pooling radio-tracking points across squirrels, because sample sizes were similar (Aebischer *et al.*, 1993) and habitat use and availability patterns were similar (Thomas and Taylor, 1990) due to dominance (83%) of ponderosa pine in BHNF.

RESULTS

Home range.—We radio-collared 59 (34 males and 25 females) northern flying squirrels, of which, 49 (30 males; 19 females) of the squirrels tracked had ≥15 radio-tracking locations. Males occupied larger 100% MCP areas (mean = 11.23, SE = 1.48 ha) than females (mean = 6.91, SE = 0.94 ha; $Z = -2.29$, $P = 0.02$) (Table 1). Northern flying squirrels in the northern hills occupied more than twice the area of squirrels in the southern hills ($Z = -3.25$, $P < 0.001$) and central hills ($Z = -2.98$, $P = 0.003$) (Table 1). In the northern hills, northern flying squirrels occupied a larger area and home ranges overlapped more than in the southern hills or central hills.

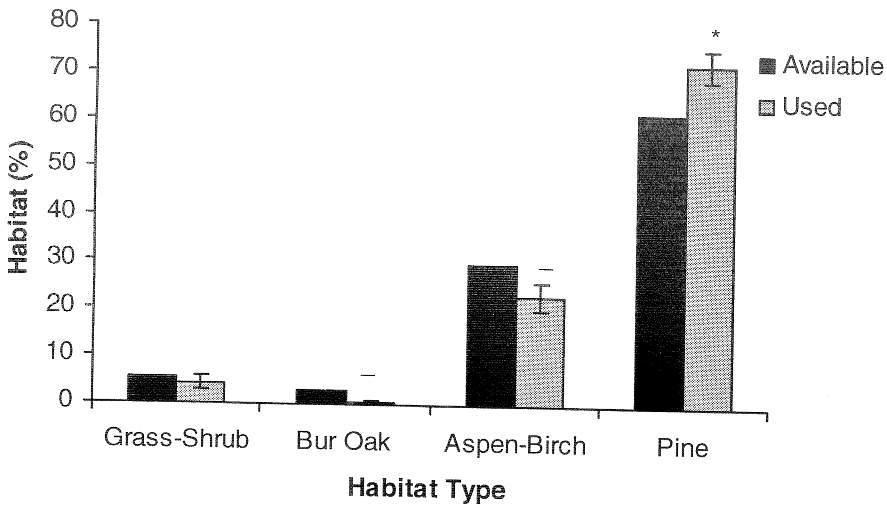

FIG. 2.—Comparison of proportion of each habitat type used to proportion of habitat available within MCP home ranges of northern flying squirrels with ≥10 radio-tracking locations in the Black Hills National Forest (May through Aug. 2005–2007). Error bars represent Bonferroni confidence interval. Minus (−) denotes habitat used less than expected and asterisk (*) denotes habitat used more than expected (P = 0.05)

Habitat use.—There were 54 northern flying squirrels (30 males; 24 females) with ≥10 radio-tracking locations used in the habitat use analysis. Within home ranges, there was a difference in the proportion of used and available habitat types ($\chi^2 = 27.09$, $P < 0.0001$). Northern flying squirrels in BHNF selected ponderosa pine, but not aspen-birch and bur oak (Fig. 2). No difference was found between proportion of used and available grass-shrub habitat. Within home ranges squirrels selected structural classes 3C and 4B, but avoided classes 1–2 and 3B (Fig. 3). There were no differences in proportion of used and available structural stage classes 3A, 4A and 4C (Fig. 3).

Males and females exhibited habitat selection and avoidance. Males and females both selected pine habitat. Males avoided grass-shrub, bur oak and aspen-birch, while females avoided aspen-birch. There was no difference in proportion of used and available grass-shrub habitat for females. None of the females in the analysis were tracked to bur oak. Males and females exhibited selection and avoidance of structural classes. Males selected structural class 3C and 4B and avoided class 1–2. Females selected structural class 4C and no difference was detected 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 fewer snags (Table 2). Aspect was used in similar proportion to availability.

DISCUSSION

Home range.—Home range size for male and female northern flying squirrels and average home range size for BHNF falls in the middle of the range for other study areas (Table 3). Males usually occupy a significantly larger area than females (Martin and Anthony, 1999; Cotton and Parker, 2000; Meyer *et al.*, 2005), as was found in this study. This study, as well as other studies, have found home ranges of male northern flying squirrels overlapped the home ranges of several females, which increases male breeding potential (Carey *et al.*, 1997;

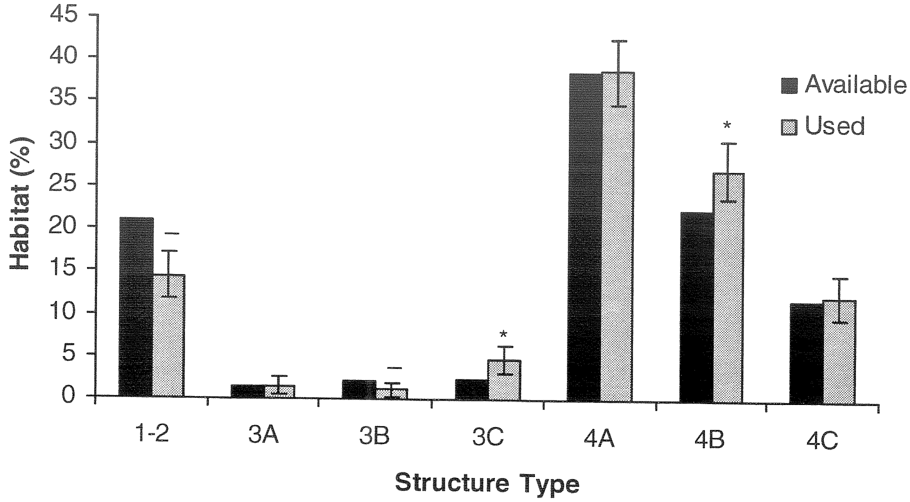

FIG. 3.—Comparison of proportion of each structural stage used to proportion of structural type available within MCP home ranges of northern flying squirrels with ≥10 radio-tracking locations in the Black Hills National Forest (May through Aug. 2005–2007). Error bars represent Bonferroni confidence interval. 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

Martin and Anthony, 1999). Males travel farther between dens (Hough, 2008) presumably to be closer to optimal food availability within their home range, which allows for increased foraging efficiency and quick escape cover from predators (Carey *et al.*, 1997; Martin and Anthony, 1999). Females may have smaller home ranges to remain close to maternal nests.

Several studies of 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). We found a higher density of northern flying squirrels in the northern BHNF (Hough, 2008), therefore, we expected home range size to be similar or smaller than in the central and southern hills. However, home range size for squirrels in the northern

TABLE 2.—Continuous variables tested for differences between means of northern flying squirrel tracking locations (1243 points) and hectares available within home ranges (414 ha) in the Black Hills National Forest (May through Aug. 2005–2007). See methods for description of habitat variables

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

[a] Means tested with Wilcoxon rank sums (P ≤ 0.05)

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

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

[a] Study did not differentiate between males and females

hills was more than twice as large as the southern and central hills. The contradiction in density and home range size in the northern hills could be due to resource availability. Smith (2007) summarized that home range size is associated with habitat quality and food resources. In xeric forests truffle abundance biomass and species composition are highest in riparian areas (Meyer and North, 2005). In drier sites in the west, squirrels appear to be associated with riparian areas with cooler and wetter conditions (Meyer *et al.*, 2005, 2007), because fungus composition and abundance may be related to moisture levels (Rillig *et al.*, 2002). Southern BHNF is classified as Dry Coniferous Forest and northern hills is classified as Mesic Coniferous Forest (Marriott *et al.*, 1999). Therefore, squirrels in the southern hills may be limited to cooler and wetter areas where fungus grows. The northern BHNF, is a Mesic Coniferous Forest, which typically support higher population densities than xeric forests (Lehmukuhl *et al.*, 2006; Hough, 2008). Microhabitat use in mesic forests is not restricted to riparian areas (Carey *et al.*, 1999), which may explain why the northern BHNF with a higher population density had a larger average home range size than the western and southern BHNF.

Habitat use.—Flying squirrels were tracked throughout their active period to determine habitat selection, as well as occasionally during the day to determine nesting habitat selection. Northern flying squirrels selected pine within their home ranges. Pine dominated habitat provides good foraging habitat because the two primary food sources consumed by northern flying squirrels are hypogeous fungus, which are associated with conifers (Weigl, 1978; Maser *et al.*, 1985; U.S. Fish and Wildlife Service, 1990; Pyare and Longland, 2001) and pine seeds. In mixed–hardwood-conifer forest or at the ecotone of hardwood and coniferous forests they use drays almost exclusively in conifers (Menzel *et al.*, 2004; Mowrey and Zasada, 1984; Hough, 2008).

Northern flying squirrels in BHNF avoided aspen-birch, bur oak and grass-shrub habitats. 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; Loeb *et al.*, 2000). Aspen and birch habitat may not be important foraging habitat; however, aspen and birch are important for den sites. Northern flying squirrels frequently use hardwoods (*e.g.*, aspen and birch) (Weigl, 1978; U.S. Fish and Wildlife Service, 1990; Hough, 2008), where cavities are readily created by primary excavators and natural formation (Carey and Gill, 1983; Menzel *et al.*, 2004; Holloway, 2006;

Holloway and Malcolm, 2007). In the Black Hills, not only were snags important for cavity nests, but all live tree cavities were in aspen and birch trees (Hough, 2008). While bottomlands with aspen and birch provide nutrient-rich, cool and moist soils for fungal growth, many mycorrhizal fungus are specialists with conifers (Loeb *et al.*, 2000). Menzel *et al.* (2006b) found that several of the squirrels they tracked denned during the day in hardwood patches and foraged during the evening in spruce of mixed spruce-northern hardwood patches. In this study we also observed this, with squirrels tracked to bottomlands of aspen and birch during the day and ponderosa pine dominated slopes and ridges during the night. Despite our findings, we believe aspen and birch habitat is important for northern flying squirrels in BHNF, but due to the dominance of nighttime tracking locations compared to daytime locations, the importance of pine for foraging habitat overshadows importance of aspen and birch as nesting habitat.

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. Across their range northern flying squirrels have not consistently been found to be associated with oak habitat and within BHNF further research would need to be conducted to determine habitat suitability. Grass-shrub habitat would not provide optimal foraging habitat for northern flying squirrels, because this habitat does not provide hosts for fungal growth or other favored food sources, in addition there is a lack of nest sites and protection from predators.

Northern flying squirrels in the BHNF were associated with areas with larger trees and more canopy cover within their home ranges. This selection may be related to being associated with pine habitat because pine trees are the largest trees in the BHNF and most abundant conifer. Larger trees indicate mature trees, which provide food sources through seeds and established mycorrhizal community (Fisher and Wilkinson, 2005), and squirrels are associated with larger trees for den sites (Carey *et al.*, 1997; Cotton and Parker, 2000; Bakker and Hastings, 2002; Meyer *et al.*, 2005). Large live pine trees are important for dray nests within BHNF (Hough, 2008). Mycorrhizal fungi fruiting bodies, truffles, appear to be most abundant in association with larger and older living trees (Weigl, 2007). Also, mycorrhizal fungus is often clumped and short-lived, therefore relatively dense canopies, large tall trees and open midstories are important for squirrels to move through their home range efficiently and safely (Vernes, 2001). Canopy cover is advantageous for northern flying squirrels because overstory cover protects squirrels foraging on the ground from aerial predators, and also provides an escape route from ground predators (Carey *et al.*, 1997).

In this study northern flying squirrels were found to be associated with areas that have a lower density of snags within their home range. However, across their range northern flying squirrels have been found to be highly associated with snags for denning (Carey *et al.*, 1997; Cotton and Parker, 2000; Bakker and Hastings, 2002; Menzel *et al.*, 2004; Meyer *et al.*, 2005), including BHNF (Hough, 2008). The study design has consistently identified important habitats flying squirrels are associated with for foraging and failed to identify important nesting habitats.

Management implications.—Overall, mature pine habitat was found to be optimal habitat for nighttime activity. Primarily providing closed canopy for protection from aerial predators (Carey *et al.*, 1997) and an open midstory for moving efficiently and safely (Vernes, 2001) throughout their active period. Also, mature pine provides food sources through seeds and established mycorrhizal community (Fisher and Wilkinson, 2005), in addition large live pine trees are important for dray nests (Hough, 2008).

The significant nesting habitats were overshadowed by the dominance of nighttime tracking locations in pine habitat. Northern flying squirrels frequently use hardwoods (*e.g.*, aspen and birch), where cavities are readily created by primary excavators and natural formation (Carey and Gill, 1983; Menzel *et al.*, 2004; Holloway, 2006; Holloway and Malcolm, 2007). In the BHNF all live tree cavities were in aspen and birch trees (Hough, 2008). Cavities in live trees may be more advantageous than snag cavities because overhead canopy provides protection from weather and predators (Carey *et al.*, 1997). In addition, live trees containing cavities persist longer and are sturdier than snags (Carey *et al.*, 1997). 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 (Weigl, 2007). Snags are also an important denning resource in BHNF. Snags comprised only 6.6% of the available trees; however, almost half (45.8%) of northern flying squirrel nests were located in snags (Hough, 2008).

Future research should concentrate efforts in spruce-dominated habitats within the BHNF, 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, b). Research should also concentrate efforts in the limited bur oak habitat to determine flying squirrel use of this habitat type.

There is a lack of mycological research on hypogeous fungus and mycophagous small mammals in BHNF. 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). We recommend further research collecting small mammal feces to identify fruiting times, composition, distribution and abundance of fungus throughout the BHNF. This data would provide a better understanding of the role flying squirrels play as a mycophagous small mammal in BHNF. Gabel *et al.* (2006) collected and examined scat from northern flying squirrels in the northern BHNF. To better understand the differences in habitat use between Mesic Coniferous Forest in northern BHNF and Dry Coniferous Forest in southern BHNF, research should focus on fungus composition and abundance throughout BHNF. 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.

The results of this study contribute to the knowledge gap for populations of northern flying squirrels at the southern portion of their range, such as the BHNF population (Smith, 2007; Weigl, 2007). Understanding resources requirements is important for isolated populations in intensively managed forests, because across their range northern flying squirrels play an important role in improving forest health through dispersal of mycorrhizal fungus and management decisions can greatly impact the population.

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