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Summer Nest Tree Use by 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 nesting ecology of this population. We radio-collared 59 northern flying squirrels and collected a daytime nest location every 2–4 wk during May through Aug., 2005 through 2007. The radio-collared northern flying squirrels used 133 different nests, including drays in live trees, cavities in live trees and cavities in snags. We examined distance between consecutively located nests and characteristics of nest trees to random and available trees within the northern flying squirrels' home ranges. The distance between consecutively located nests was farther for males than females. Sixty-eight percent of the nests used were in cavities. Snags and larger trees were selected for nest sites more than expected based on availability. This study will help managers understand an aspect of microhabitat resource use by northern flying squirrels in ponderosa pine (*Pinus ponderosa*) dominated habitat of BHNF and an isolated population at the southern edge of their range.

INTRODUCTION

Nest trees are an important habitat resource for northern flying squirrels (*Glaucomys sabrinus*) and are used as maternal nests, daytime resting locations and protection from inclement weather and predators (Carey *et al.*, 1997). In some areas, nest site availability may 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 typically nest in drays or cavities. Drays are external nests, consisting of intertwining twigs or smaller branches constructed on branches or boles or on witches' broom. Northern flying squirrels occupy cavities created naturally in live trees from decayed branch scars of hardwoods or in snags (Thomas *et al.*, 1979). Northern flying squirrels are secondary cavity users and will also occupy cavities created by woodpeckers (Wells-Gosling and Heaney, 1984), particularly in hardwoods (Weigl and Osgood, 1974; Holloway, 2006). 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). Cavities and drays are lined with lichens, leaves and other materials for insulation (Wells-Gosling and Heaney, 1984; Hayward and Rosentreter, 1994; Carey *et al.*, 1997).

Northern flying squirrels use live trees and snags, that are older, larger and taller (relative to availability) throughout their range (Weigl and Osgood, 1974; 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 nest site selection vary regionally due to different forest community composition and land use or management history (Weigl and Osgood, 1974; Carey *et al.*, 1997; Cotton and Parker, 2000; Hackett and Pagels, 2003; Menzel *et al.*, 2004; Smith, 2007). Because northern flying squirrels use a range of nest types and structures within and among study areas this species may be opportunistic with respect to nest site selection (Rosenberg and Anthony, 1992; Carey *et al.*, 1997; Cotton and Parker, 2000; Hackett and Pagels, 2003; Smith, 2007).

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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, 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), involving the squirrels in 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.

Despite the increase in northern flying squirrel research over 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 (*Pinus ponderosa*: 83% (USDA Forest Service, 2005)) 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 (*e.g.*, clear-cutting, development) which destroy extensive tracts of habitat (Koprowski, 2005; Weigl, 2007). Smith (2007) also suggested priority for researching northern flying squirrels be given to populations on the edge of the geographic distribution where knowledge is scarce.

Our objectives were to quantify local and landscape habitat features at used and available nest trees to determine important habitat features of northern flying squirrel nest use in the Black Hills. Our objective was also to determine if males and females used different types of nests, because females use the nests for maternal nests in addition to daytime resting and protection. This information will assist managers in the BHNF by providing tree and habitat characteristics important for northern flying squirrel nest use and also contribute to the limited knowledge of northern flying squirrel nesting ecology 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 approximately 1200 to 2207 m, with the forested region extending to 2102 m (Froiland, 1990).

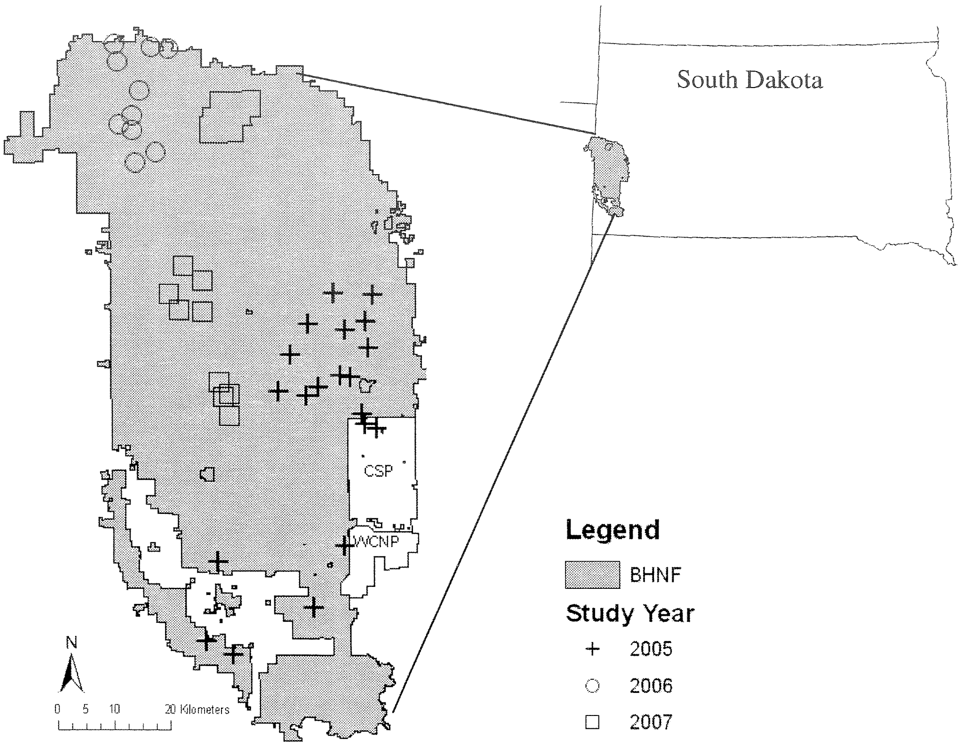

FIG. 1.—Location of trap sites for northern flying squirrels in the Black Hills National Forest (BHNF) (May through Aug. 2005–2007). Custer State Park (CSP) and Wind Cave National Park (WCNP) are located in the southeast portion of the Black Hills region

The southern Black Hills, has a warmer (9.3 C) and drier (45–51 cm/yr) annual climate than the northern portion of the range (7.2 C and 61–66 cm/yr; 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 (*Populus tremuloides*) and paper birch (*Betula papyrifera*) 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 (*Picea glauca*) 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 moist 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 the 2005 season. 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.

We located radio-collared northern flying squirrels with a Yagi antenna and model R2000 ATS receiver. To monitor nest use, we located all radio-collared northern flying squirrels every 2–4 wk. To determine home range size radio-collared squirrels were tracked from dusk to dawn (8 p.m. to 5 a.m.) by point sampling (Kenward, 2001). 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.

Nest habitat measurements.—We used ArcMap 9.1 (Environmental Systems Research Institute Inc., Redlands, CA) to estimate the distance between UTM coordinates taken for consecutively located nests for each northern flying squirrel. We also measured habitat variables at nest sites and at a random tree of the same species located 20 to 50 m in a random direction from the nest to directly compare flying squirrel nest trees with available trees. The random tree was the same species as the nest tree, because we wanted to eliminate potential bias due to the dominance of ponderosa pine. At each nest tree and random tree, we noted tree species, tree condition (live or snag), nest type (dray or cavity), snag decay class (adapted from Thomas *et al.*, 1979), diameter at breast height (dbh), tree height and canopy cover. We measured canopy cover using a densiometer and averaged the percent canopy cover 1 m from the tree in each of the cardinal directions. Landscape features measured at the tree location included slope, aspect and elevation.

Within a 5-m radius (ground and understory level) around the nest tree and random tree, we recorded the sapling density, dominant sapling species, understory cover and ground cover. Within a 10-m radius (overstory level) around the nest tree and random tree we recorded total tree density, live tree density, snag density, dominant tree species and species and diameter of all overstory live trees and snags. We recorded the height and decay class for all snags and calculated basal area based on trees within a 10-m radius of nest trees and random trees. We recorded nest type (cavity or dray) and nest category (live dray, live cavity or snag cavity) for flying squirrel nests only; cavities in random trees were not always obvious from the ground.

For our analyses we compared nest trees to random trees and available trees. Analyses comparing nest trees and random trees compared characteristics and composition of trees within the 10-m radii around nest trees and random trees. Throughout the paper these comparisons are denoted as "random trees." Available trees include random trees and all trees within the 10-m radii around nest trees and random trees. These analyses of available trees compare characteristics of nest trees to tree composition within the home ranges. Throughout the paper these comparisons are denoted as "available trees."

Statistical analysis.—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. To examine differences between consecutively located nests we used Wilcoxon rank sums to examine differences between sexes and Kruskal-Wallis ANOVA to examine differences between years. Fisher's exact test was used to examine the association between frequency of live and snag nest trees to available trees. Fisher's exact test was also used to examine associations of each nest type (dray or cavity) used between sexes and between years. Likelihood-ratio chi-square was used to examine associations of nest type (dray or cavity) for all nests, as well as nest type and den tree condition (live dray, live cavity and snag cavity) for each sex and each year.

Likelihood-ratio chi-square test (χ^2) was used to examine the association of each tree species used to available. Few (<1%) live oak (n = 20) were available for nest sites; there were no nests in live oak trees. There were no oak snags used or available and one spruce snag was available, but none were used as a nest site. Therefore, only aspen, birch and pine were used in the Wilcoxon rank sums test to examine associations of snags to live trees used as nests among tree species.

We used Wilcoxon rank sums test to detect differences in diameter and height of nest trees with cavities compared to nest trees with drays. We used another chi-square tests (χ^2) to examine the association between nest type (cavity, dray) and nest tree size class (4 diam classes, 3 height classes); size classes were based on current BHNF management practices (USDA Forest Service, 2005).

We used stepwise conditional logistic regression to compare nest and random trees. The data was 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 nest trees and random trees for diameter, 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 25% level were retained for further statistical analysis (Hosmer and Lemeshow, 2000). 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 conditional logistic regression model. In the stepwise model entry was set to $P = 0.05$ and removal was $P = 0.10$.

RESULTS

We tracked 59 radio-collared northern flying squirrels (34 males, 25 females) to 133 different nests (53 nests in 2005; 54 nests in 2006; 26 nests in 2007). Cavity nests were located in live aspen trees, live birch trees, and aspen, birch and pine snags. Dray nests were located in live pine and spruce trees.

Distance between nests.—There was no difference in the distance moved between nest trees by northern flying squirrels between years ($\chi^2 = 0.01$, $P = 0.99$); however, males traveled farther between nests (182.93 ± 15.85 m) than females (126.17 ± 13.46 m; $Z = -2.35$, $P = 0.02$) (Table 1). One male moved 695 m and 873 m between consecutively located nests and these distances were eliminated as outliers.

TABLE 1.—Distances between consecutively located nests used by male and female northern flying squirrels in the Black Hills National Forest (May–Aug., 2005–2007)

	Distance (m)			
	n[a]	Mean	SE	Range
Males	40	182.93*	15.85	23–437
Females	29	126.17*	13.46	21–286
Combined	69	159.07	11.24	21–437

[a] Number of distances measured between consecutively located nests
* Significant differences between males and females ($P \leq 0.05$)

Nest tree use versus availability.—Northern flying squirrels in the BHNF did not use nest sites randomly ($\chi^2 = 125.42$, $P < 0.001$). Snags (n = 57) comprised 42.9% of the nest sites and were used almost five times more than expected based on availability (7.8% of available trees; $\chi^2 = 113.47$, $P < 0.001$) (Fig. 2). Nest tree species were selected in proportion to availability ($\chi^2 = 4.07$, $P = 0.396$). There was no difference in the type of nests (dray live, cavity live, cavity snag) used between sexes ($\chi^2 = 4.40$, $P = 0.11$). The diameter of all nest trees, live trees used as nests and snags used as nests were larger than available trees of same tree condition (Table 2).

Overall, squirrels were tracked to more cavities than dray nests ($\chi^2 = 18.49$, $P = < 0.001$) Males used more cavities (18 drays and 55 cavities) than females (25 drays and 35 cavities), but there was no difference between years (2005: 14 drays and 38 cavities; 2006: 18 drays and 37 cavities; 2007: 11 drays and 15 cavities; $\chi^2 = 1.85$, $P = 0.40$). More specifically males were associated with cavities in snags ($\chi^2 = 9.31$, $P = 0.01$), while females used similar types of nests (live dray, live cavity and snag cavity; $\chi^2 = 1.61$, $P = 0.45$) (Fig. 3).

Trees with dray nests were larger (n = 43, 36.04 ± 2.52 cm) than nest trees with cavities (n = 90, 25.02 ± 0.87 cm; $Z = 4.22$, $P < 0.001$). Nest trees with drays (n = 43, 25.52 ±

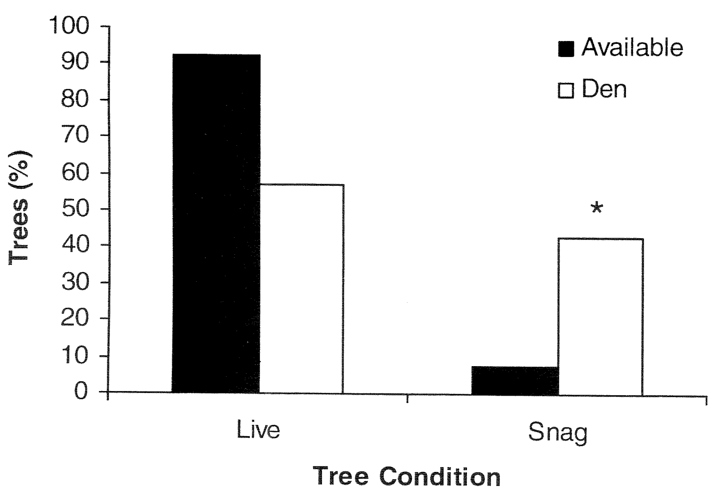

FIG. 2.—Proportion of live trees (n = 76) and snags (n = 57) used as nests by northern flying squirrels compared to available live trees (n = 3,104) and snags (n = 262) in the Black Hills National Forest (May through Aug. 2005–07). Asterisk (*) indicates tree condition was used more than expected ($P \leq 0.05$)

TABLE 2.—Comparison of overall diameter at breast height (dbh), live tree dbh and snag dbh between northern flying squirrel nest trees and random trees or available trees in the Black Hills National Forest (May through Aug. 2005–2007)

	Nest		Random			Available		
	n	mean ± SE	n	mean ± SE	P[a]	n	mean ± SE	P[b]
dbh (cm)	133	28.58 ± 1.09	133	27.20 ± 1.06	0.37	3366	23.58 ± 0.15	<0.001*
Live dbh (cm)	76	31.34 ± 1.61	93	28.61 ± 1.32	0.22	3104	23.70 ± 0.15	<0.001*
Snag dbh (cm)	57	24.90 ± 1.23	40	23.91 ± 1.63	0.56	262	22.07 ± 0.53	<0.001*

[a] Comparison between nest trees and random trees
[b] Comparison between nest trees and available trees
* Indicates a significant difference ($P \leq 0.05$)

1.04 m) were more than twice as tall as nest trees containing cavities (n = 90, 11.41 ± 0.65 m; $Z = 7.97$, $P < 0.001$). When tree diameter and tree height were grouped into diameter and height categories, respectively, based on Forest Service management categories, dray nests were found in larger and taller trees than nest trees with cavities (Fig. 4).

Results comparing nest trees and random trees were not significant for diameter, live tree diameter, snag diameter, snag decay class, total tree height, live tree height, snag height, slope, aspect, elevation or canopy cover. Results were not significant for density of saplings, sapling species, understory cover or ground cover within the 5-m radius around nests and random trees. Within the 10-m radius around nest trees and random trees, total tree basal area was marginally higher surrounding nest trees ($Z = 2.00$, $P = 0.05$). Within the 10-m radius around nest trees and random trees, the results were not significant for dominant tree species, total tree density, total live trees, live basal area, total snags, snag basal area,

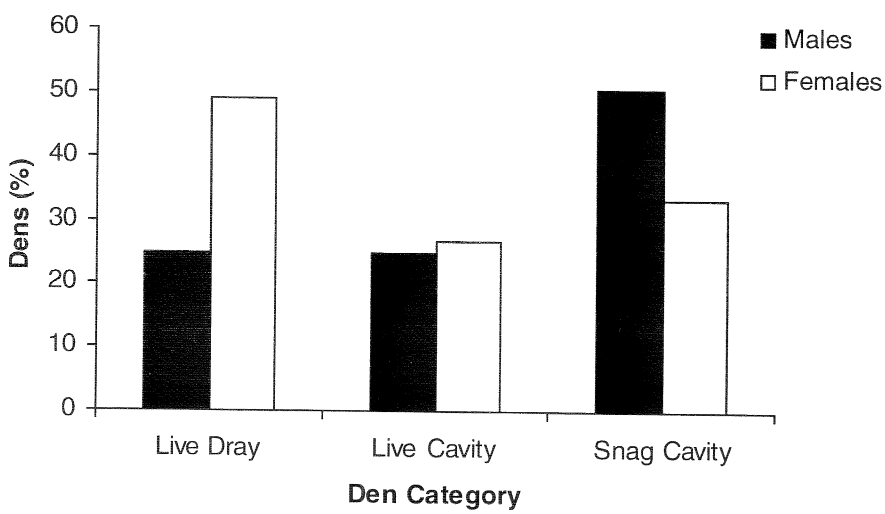

FIG. 3.—Nest category use by male (n = 73) and female (n = 60) northern flying squirrels in the Black Hills National Forest (May through Aug. 2005–2007)

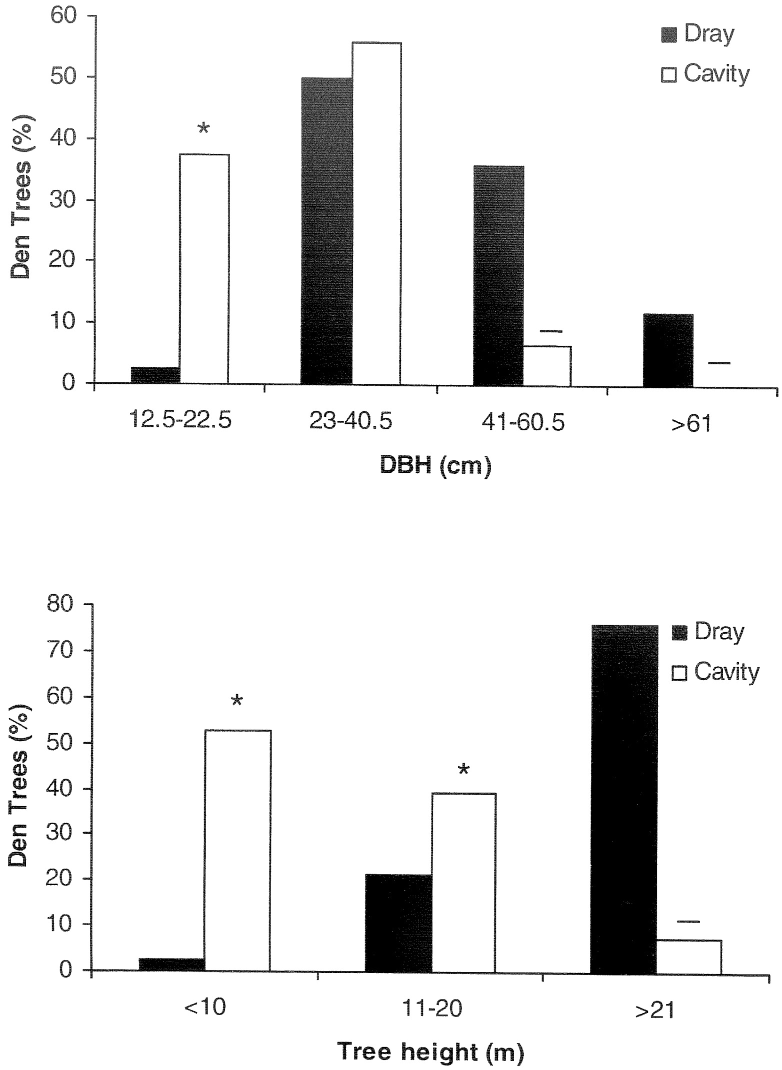

FIG. 4.—Number of northern flying squirrel drays (n = 43) and cavities (n = 90) by tree diameter at breast height (dbh) (cm) and height (m) classes in the Black Hills National Forest (May through Aug. 2005–2007). Asterisk indicates cavities used significantly more than drays, and dash indicates cavities used significantly less than drays for each dbh and height class ($P \leq 0.05$)

total conifers, conifer basal area, total deciduous trees or deciduous basal area. Total basal, percent understory and live basal area all had $P < 0.25$, therefore, these variables were considered for the stepwise conditional regression model. Of these variables, the only significant variable in the model was total tree basal area surrounding the nest tree (regression coefficient ± SE = 1.86 ± 0.68; Odds ratio (±95% CI) = 6.40 ± (1.70, 24.08); $P = 0.01$).

DISCUSSION

Distance between nests.—Distance moved between dens is highly variable for northern flying squirrels (Cotton and Parker, 2000; Hackett and Pagels, 2003). The squirrels change nests presumably in response to seasonal changes in food availability (Menzel *et al.*, 2006), change in weather (Mowrey and Zasada, 1984), buildup of parasites or for predator avoidance (Carey *et al.*, 1997). Northern flying squirrels in the BHNF traveled farther between nests (159 m) than in Oregon (71 m; Martin and Anthony, 1999), but similar distances as in central Appalachians (164 m; Hackett and Pagels, 2003) and northwestern British Columbia (163 m; Cotton and Parker, 2000). This difference may be a reflection of resource availability. Also, other studies tracked squirrels during various seasons, we tracked only during summer and did not track as frequently during the daytime, thus the squirrels may be using other nests between those we tracked them to.

During this study, males moved farther between nests (182.9 m) than females (126.2 m), as was found by Carey *et al.* (1997) in Pacific Northwest and Meyer *et al.* (2005) in Sierra Nevada. This greater distance may be related to home range size as males occupy a significantly larger area than females in this study area (Hough, 2008) and across their range (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). Males may travel farther between nests to optimize food availability within their home range, thereby increasing foraging efficiency and reducing predation risk (Carey *et al.*, 1997). Females may have smaller home ranges to remain close to maternal nests. Females will change nests if the maternal nest is disturbed or infested with parasites (Carey *et al.*, 1997). Litter sizes for northern flying squirrels are two to four (range one to five) across their range (Muul, 1969), therefore females choose alternate nests close to the maternal nests because of the risk and energy required to carry young between nests. During our study females were observed lactating and some were observed with young. Also, on several occasions we observed two squirrels nesting together, they were not always a male-female pair, there were never more than two collared squirrels together and they did not nest together the entire summer.

Nest tree use versus availability.—Northern flying squirrels are usually generalists in nest site selection, but throughout their range, including BHNF, they have been found to select nest trees (live and snags) that are older, taller and larger than what is available (Carey *et al.*, 1997; Cotton and Parker, 2000; Bakker and Hastings, 2002; Menzel *et al.*, 2004; Meyer *et al.*, 2005). Cavities (in snags and live trees) are more likely to occur in larger trees because primary excavators prefer larger trees for nesting (Thomas *et al.*, 1979), and larger, older trees are more prone to decay, resulting in snags and cavity formation (Lentile *et al.*, 2000). We could not determine if northern flying squirrels in BHNF used live hardwoods with cavities or cavities in general (live trees or snags) more than expected based on availability because of the difficulty of accurately detecting cavities in random live hardwoods.

Northern flying squirrels in the BHNF used tree cavities for nesting more frequently than drays, 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 nests were located in snags. Cavities provide better protection from weather (Carey *et al.*, 1997; Maser *et al.*, 1981; Menzel *et al.*, 2004) and predators (Carey and Sanderson, 1981) than external nests.

Males were associated with cavities, more specifically, males were associated with cavities in snags, while females showed no difference to den type selection. We expected females to select cavities over drays for maternal nests because of the extra protection from weather and predators provided with cavities (Carey *et al.*, 1997; Holloway, 2006; Ransome and Sullivan, 2004). 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. During our study lactating females were observed using cavities as well as drays, we speculate that being at the southern edge of their range females may not require the thermal protection cavities offer; however, the protection from predators would still be important. Several studies suggest other reasons for nest site selection, such as selecting dens near red squirrel (*Tamiasciurus hudsonicus*) middens (Vernes *et al.*, 2004), proximity to food patches (Hackett and Pagels, 2003; Menzel *et al.*, 2004), or proximity to water sources (Meyer *et al.*, 2005).

Northern flying squirrels are often associated with cavities in snags, but in some areas prefer cavities in live trees over snags (Carey *et al.*, 1997; Cotton and Parker, 2000). 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 Black Hills, not only were snags important for cavity nests, but all live tree cavities were in aspen and birch trees. 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).

In mixed-coniferous-hardwood forests and coniferous forests northern flying squirrels use drays almost exclusively in conifers (Mowrey and Zasada, 1984; Menzel *et al.*, 2004; Holloway and Malcolm, 2007), this was also the case in BHNF. All drays were found in live pine and spruce, which are the tallest tree species in the BHNF, reaching 35 m and 20 m, respectively (Larson and Johnson, 1999). Therefore, dray nests were in trees that were larger in diameter and taller (averaging twice the height) than trees containing cavities, which was also found in the central Appalachians (Menzel *et al.*, 2004). Dray nests were found in the canopy of the nest tree, resulting in dray nests being higher than cavity nests, as was found in other studies (Menzel *et al.*, 2004; Holloway and Malcolm, 2007). Ponderosa pines are self-pruners (lower branches of the tree die off because of lack of sunlight and the tree naturally sheds the dead branches), so dray nests in pines were in the top third of the tree. Taller pines provide a greater distance from the ground, resulting in lower predation risk (Carey *et al.*, 1997). Also, larger and taller trees containing cavities are limited in the BHNF. All dens were in cavities of live aspen and birch or snags of aspen, birch and pine. Aspen and birch grow only to 15 m (Larson and Johnson, 1999) and only three pine snags were >20 m tall in our study plots. Spiering and Knight (2005) found that smaller snags were common in the BHNF and larger diameter size classes were rare (approximately 3%).

Management implications.—The USDA Forest Service sets requirements in the BHNF for the minimum number and size of snags per acre for pine, spruce and other dominant overstory species. Requirements also are set for green tree (live tree) retention for snag recruitment. Spiering and Knight (2005) found a high number of smaller diameter snags and few snags in the larger diameter size classes in the BHNF. Snag densities, as well as the number of cavity nesting birds have decreased from historical records (Spiering and Knight, 2005). Snags in the BHNF are used by at least 23 bird and 9 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 (Lentile *et al.*, 2000).

Maintaining and increasing habitat for primary cavity excavators is important to secondary cavity users, such as the northern flying squirrel. In the Black Hills, several woodpecker species excavate and nest within live aspen and birch trees (Shepperd and Battaglia, 2002), providing increased nesting opportunities for secondary cavity users. Northern flying squirrel home ranges in the BHNF include areas of aspen and birch where cavities are readily available for nests, as well as a ponderosa pine component where the fungi consumed by the northern flying squirrels readily grows (Hough, 2008). Home ranges with a mix of aspen, birch and pine suggests that either snags are not available for nests or northern flying squirrels are selecting cavities in live aspen and birch because of the advantages provided by cavities in live trees.

There are several management practices that can increase the number of cavities available, such as retaining hardwoods with cavities and snags, and creating snags and cavities. 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 diameter 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 m above ground and remove lower limbs (Bull and Partridge, 1986). Cavities also can be created in live trees using mechanical methods (Carey and Gill, 1983).

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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