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# Nest Tree Use by the Endangered Virginia Northern Flying Squirrel in the Central Appalachian Mountains

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ABSTRACT.—Little is known about nest tree use of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). Because nesting sites could be a limiting factor, it is important to understand the denning ecology to further manage and protect this subspecies. We compared characteristics of nest trees used by Virginia northern flying squirrels with randomly selected trees during summer and fall of 2000 and 2001. We tracked 13 Virginia northern flying squirrels to 59 nest trees. The squirrels used an average of 3.6 nest trees/month, switching trees frequently. Sixty-nine percent of the nests were in cavities and 31% were leaf nests. Yellow birch (*Betula alleghaniensis*) and Fraser magnolia (*Magnolia fraseri*) were selected for nest trees more than expected based on availability. A large portion of nest trees were in larger and taller trees than trees in the surrounding area. There also was a significant number of trees located next to or near skidder and hiking trails. Although a large number of nest trees were similar across sites, there was variation in the characteristics of nest trees used, suggesting that Virginia northern flying squirrels may not be as specialized in nest tree selection as indicated by previous studies.

## INTRODUCTION

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) is a noctural sciurid that inhabits disjunct high elevation "islands" in the central Appalachians of eastern West Virginia and western Virginia (Wells-Gosling and Heaney, 1984). In 1985, due to natural and anthropogenic fragmentation of habitat and vulnerability of the subspecies, the U.S. Fish and Wildlife Service (USFWS) added the Virginia northern flying squirrel to the endangered species list (USFWS, 1985). Because several factors threaten the Virginia northern flying squirrel, such as degradation and loss of montane boreal forest habitat, introduction of forest insect pests (*e.g.*, balsam wooly adelgid, *Adelges piceae*) and poorly known habitat requirements (USFWS, 1990), conservation efforts have been difficult.

There is a paucity of quantitative information about the characteristics of nest trees used by Virginia northern flying squirrels in the central Appalachians. Research on these characteristics, in addition to other habitat requirements, was a major objective outlined in the strategy for recovery in the Appalachian Northern Flying Squirrel Recovery Plan (USFWS, 1990). Limited information available about nest trees used by this subspecies was obtained either from anecdotal accounts, preliminary studies or inferred from research conducted in other areas of the species' range ((??)Cowen, 1936; Urban, 1988; Cotton and Parker, 2000). Because of differences in habitat type and forest structure among regions where each subspecies of northern flying squirrel occurs, habitat requirements of the Virginia northern flying squirrel most likely differ from other subspecies of *Glaucomys sabrinus*.

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Throughout their range, northern flying squirrels use both tree cavities and leaf nests (Howell, 1918; Kittredge, 1928; Bailey, 1929; Cowan, 1936; Weigl and Osgood, 1974; Weigl, 1978; Urban, 1988; USFWS, 1990; Weigl *et al.*, 1999). During summer, northern flying squirrels in the Pacific Northwest and southern Appalachians use a combination of leaf nests and cavities (Cowan, 1936; Weigl and Osgood, 1974; Urban, 1988; USFWS, 1990; Carey *et al.*, 1997; Weigl *et al.*, 1999). During winter, northern flying squirrels typically only nest in cavities (Jackson, 1961; Baker, 1983; USFWS, 1990; Weigl *et al.*, 1999; Cotton *et al.*, 2000). Flying squirrels use leaf nests and cavities for a variety of purposes including diurnal sleeping sites, feeding stations during nocturnal foraging bouts and as nests for raising young (Weigl and Osgood, 1974; Wells-Gosling and Heaney, 1984). Research shows that southern flying squirrels will nest communally, possibly to reduce energy expenditure during cold weather (Stapp *et al.*, 1991; Stapp, 1992; Merritt *et al.*, 2001). Although northern flying squirrels are generally less gregarious than southern flying squirrels, communal nesting has been documented (Wells-Gosling and Heaney, 1984).

In the southern Appalachians of North Carolina and Tennessee, Weigl *et al.* (1999) found that natural cavities used by Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*) were either in abandoned woodpecker holes or cavities formed from decay. They found that yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*) were the most common tree species used for nesting. In both the Pacific Northwest and southern Appalachians, nest heights have been reported from 1 to 19 m above ground (Bailey, 1929; Jackson, 1961; Weigl and Osgood, 1974). In West Virginia, Urban (1988) found leaf nests exclusively in red spruce (*Picea rubens*) or eastern hemlock (*Tsuga canadensis*) at an average height of 12 m.

Aside from these general characteristics of northern flying squirrel nest trees, little else is known about nest site requirements. A better understanding of the nest site requirements of Virginia northern flying squirrels is necessary for the management of the fragile and fragmented habitat of this subspecies and for its eventual recovery and de-listing. Knowing tree characteristics required for nesting by Virginia northern flying squirrels is critical, especially in existing landscapes undergoing development or in industrially managed forests. Additionally, a better understanding of nest site requirements could allow forest managers to more effectively restore high elevation spruce forests for the benefit of the Virginia northern flying squirrel in addition to other species such as the northern goshawk (*Accipiter gentilis*) and the saw-whet owl (*Aegolius acadicus*). Our objective was to quantitatively compare the characteristics of Virginia northern flying squirrel nest trees to trees randomly located across the central Appalachian landscape to determine landscape and tree characteristics most influential in nest-tree selection.

## METHODS

*Study area.*—Our study was conducted from May to September 2000 and from May to August 2001 on the Mead Westvaco Ecosystem Research Forest (MWERF) near Adolph, West Virginia (Randolph County) and on the Monongahela National Forest (MNF) managed by the USDA Forest Service near Parsons, West Virginia (Randolph and Tucker counties). Both the MWERF and MNF are located in the Allegheny Mountain and Plateau physiographic subsections of the central Appalachians (Fenneman, 1938; Stephenson, 1993). Sites on the MNF included Stuart Knob, Canaan Heights and McGowen Mountain areas (Fig. 1). The MWERF is a 3360 ha intensively managed area forested with hardwood, mixed hardwood, conifer and non-forested tracts, whereas the MNF is a 367,455 ha forest that contains a wide variety of forest conditions from unmanaged native second-growth with legacy trees to

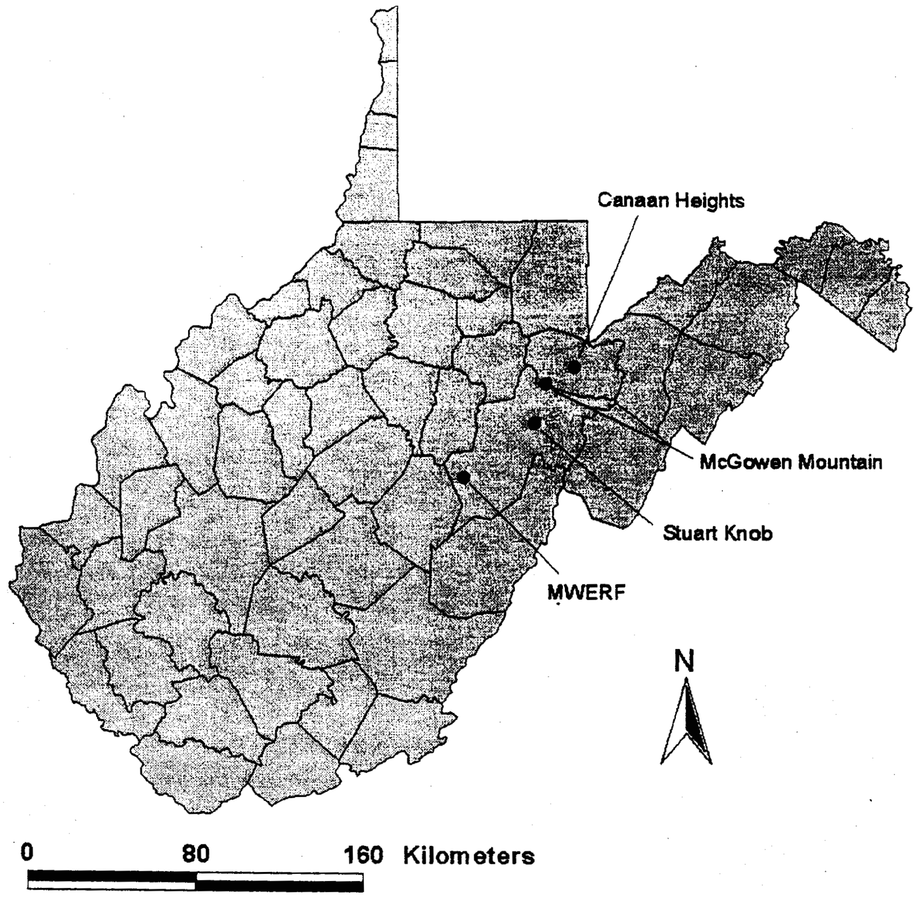


FIG. 1.—Location of study sites used during our study in West Virginia during the summer 2000 and 2001

intensively managed forests such as conifer plantations and conditions similar to the MWERF.

Regionally, topography consists of northeast to southwest-running steep ridges divided by narrow valleys (Stephenson, 1993). Elevations across the study sites range from 700 to 1300 m. The climate is generally cool and moist with a short (<140 d) growing season and annual precipitation ranging from 120 to 150 cm much of which occurs as snow in the winter months (Strausbaugh and Core, 1978; Stephenson, 1993). The overstory forest community is comprised of red spruce, eastern hemlock, sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch, American beech and black cherry (*Prunus serotina*). Mid- and understory vegetation are predominantly American beech, red spruce, red maple, yellow birch, eastern hemlock and rosebay rhododendron (*Rhododendron maximum*).

Although the species composition of all four study sites is similar, with the exception of Canaan Heights, there is some variation in forest structure and age class distribution. The MWERF is managed with both even- and uneven-aged techniques. Stands, defined as neighboring groups of trees with similar species, age classes and conditions, include recent (<15 y) clearcuts, deferment cuts, sawtimber cuts as well as control areas that have not been harvested in approximately 60 y. Stuart Knob and McGowen mountains were both uneven-aged sites that had not been harvested or thinned since the early 1920s. These stands are characterized by large overstory red spruce and northern hardwoods with a dense midstory and understory. Finally, Canaan Heights is an even-aged plantation (>1000 ha) that was planted in the early 1900s with Norway spruce (*Picea abies*). The overstory is dominated by Norway spruce and the midstory and understory are sparsely populated with northern hardwood species. Both the MWERF and Canaan Heights are fragmented by an extensive network of gravel roads and skidder trails.

*Nesting sites.*—We captured Virginia northern flying squirrels both in wooden nest boxes (30 × 23 × 36 cm) and Tomahawk® live traps (14 × 14 × 41 cm; Tomahawk, WI). We placed traps on the ground next to logs and stumps and baited them with a mixture of peanut butter, rolled oats and molasses. To reduce exposure during periods of cold weather, we placed polyfiber fill in each trap. We set traps in the evening (1900 h) and checked the traps in the morning (0600 h) to reduce captures of non-target diurnal species such as red squirrels (*Tamiasciurus hudsonicus*) and eastern chipmunks (*Tamias striatus*). Nest boxes were placed throughout the study sites from 1985 to 1996 by the West Virginia Division of Natural Resources and the United States Department of Agriculture (USDA) Forest Service to determine presence or absence of Virginia northern flying squirrels. Nest boxes were attached to the boles of trees at heights ranging from 2 to 6 m (Stihler *et al.*, 1995). We monitored nest boxes every 2 wk throughout the study period (Carey and Gill, 1983).

We recorded body measurements and information from each flying squirrel captured including sex, mass, hind foot length, age and reproductive condition. Age was determined on the basis of mass and pelage (Witt, 1992). We considered individuals to be adults if their mass was >75 g. We determined reproductive condition by examining external genitalia. For recapture identification, we attached one uniquely numbered ear tags (No. 1005-1, National Band & Tag Co., Newport, KY) to each squirrel captured. We differentiated between captured northern and southern flying squirrels (*Glaucomys volans*) by examining the hind foot measurement and pelage coloration. Adult northern flying squirrels had hind foot measurements >34 mm and had gray or lead colored fur ventrally (Wells-Gosling and Heaney, 1984).

We attached SM1-BR radio collars (4.0–5.0 g, frequency 150–151 MHz; AVM Instruments Company, Ltd., Colfax, CA) to 13 Virginia northern flying squirrels. To reduce the amount of stress placed on the animal and to ensure proper fitting and attachment of the radio collar, we anesthetized flying squirrels with the short-acting inhalant anesthetic Halothane® (Halocarbon Laboratories, River Edge, NJ) prior to ear tag and radio collar attachment. To anesthetize the flying squirrels, we soaked a cotton ball in Halothane® and placed it in a clear plastic container with the flying squirrel. We visually monitored the flying squirrel until it was sedated (approximately 1–2 min). Once sedated, we collected measurements and attached the ear tag and radio collar. Prior to release, we monitored captured flying squirrels for approximately 15 min in a catch bag to ensure they had recovered completely. We released flying squirrels at the capture sites. All anesthesia and tagging methods were approved by the West Virginia University Animal Care and Use Committee (permit # 9912-01).

We located nest trees of radio-collared squirrels by homing in on the telemetry signal during the day using Wildlife Materials TR4-2000S receivers (Carbondale, IL) and 3-element Yagi antennas. We verified nest locations at dusk by watching for flying squirrel emergence. We located nest trees of all flying squirrels daily for the life of the radio collar. Once a nest tree was located, we marked it with flagging to ensure proper identification for later vegetation sampling. We did not examine nest trees until the flying squirrel had vacated the tree.

To determine nest-tree selection, we took quantitative measurements from confirmed nest trees and the surrounding habitat. We established a 0.04 ha sampling plot (11.4 m radius) around each nest tree. Within this plot, we took 30 habitat measurements including elevation, slope, aspect of land, aspect of nest entrance, nest tree species, nest type (leaf or cavity), nest size, nest tree height, diameter breast height (DBH) of nest tree, decay class (1 (low) – 4 (high)), nest height, distance to nearest overstory tree, distance to nearest understory tree, number of overstory trees, overstory basal area, number of snags, snag basal area, percent canopy cover, percent cover of midstory, seedling cover, forest floor (herbaceous vegetation) cover, moss cover, rock cover, litter type, litter depth, distance to nearest water, distance to nearest trail and overstory, midstory, and understory species composition. Our vegetation sampling techniques followed those outlined in Hayes *et al.* (1981). Trees with a DBH of $\geq$9.5 cm were considered overstory. We measured tree height and slope with a clinometer and DBH with a diameter tape. We recorded percent canopy closure as the average of 4 spherical densiometer (Forest Densiometers, Arlington, VA) readings taken at each of the 4 cardinal directions 1 m from the base of the nest tree (Vora, 1988). We measured nest entrance aspect and land aspect with a compass corrected to true north.

To determine the characteristics of the nest trees that were statistically different from the available trees, we compared measurements of nest trees to randomly located trees within the home range of each individual flying squirrel (Menzel *et al.*, 1998). Home range was determined using the adaptive kernel method and was calculated for squirrels with >30 locations (Menzel *et al.*, in review). We developed a standard protocol for selecting random trees that included selecting an accessible random point within the home range of the squirrel using a geographic information system (GIS). From this random point, we randomly selected a compass bearing and measured 100 m from that point. We located a random tree 100 m from the accessible random point obtained using GIS in case that point fell on a non-forested location (*i.e.*, road). At this location, the first overstory tree that contained a cavity or would support a leaf nest was selected as the random tree. We took the same measurements in a 0.04 ha sampling plot around each random tree as the nest trees. We tested the data for normal distribution using a Shapiro-Wilk's test (Proc Univariate, SAS Institute Inc., 1990). Because the data were not normally distributed, we used non-parametric tests where appropriate.

We compared the characteristics of nest trees and random trees using both univariate and multivariate statistical procedures. We first tested for differences between nest tree selection of male and female flying squirrels and between study years. For the univariate test, we used a non-parametric Wilcoxon test (SAS Institute Inc., 1990). To determine if tree species influenced nest tree selection by Virginia northern flying squirrels, we compared tree species used as nest sites to the species composition of random trees, as well as the tree species composition located in our circular sampling plots. We chose to include both random trees and overstory trees in sampling plots to ensure more complete representation of forest composition (Carey *et al.*, 1998; Menzel *et al.*, 1998). We compared species composition of nest trees to randomly located trees and other nearby overstory trees using the maximum likelihood *G*-test for independence (Sokal and Rohlf, 1987). To determine if Virginia northern flying squirrels selected nest trees or chose dens based on certain aspects of terrain or den opening, we determined the number of nest trees located on north (316–45°), east (46–135°), south (136–225°) and west (226–315°) facing slopes and the number of den entrances facing north, east, south and west. We compared the resulting calculations to land and den aspects of randomly located trees using the maximum likelihood *G*-test for independence. To identify the tree species or aspect that were used significantly more than expected, we examined the adjusted standardized residuals with a minimum residual distance of $\pm$3.00 for the tree species and $\pm$5.00 for the aspects to obtain a significance level of $\alpha = 0.05$ (Haberman, 1973; Aubry and Raley, 2002). Because radio-collared flying squirrels used both leaf and cavity nests, we tested for differences between the two types of nest trees using the Wilcoxon test (SAS Institute Inc., 1990). We used $\alpha = 0.05$ as a rejection criterion for all statistical tests.

For the multivariate test, we used logistic regression to compare cavity nest tree characteristics to characteristics of randomly selected cavity trees (SAS Institute Inc., 1990). To validate the logistic regression model, a jackknife procedure was used (SAS Institute Inc., 1990). We used logistic regression instead of a discriminant function analysis because of the relaxed assumptions of normality and the acceptance of both continuous and categorical variables associated with logistic regression.

## RESULTS

We tracked 13 (8 female, 5 male) northern flying squirrels to 59 nest trees during 2000 and 2001. Individuals commonly nested in the same tree for several days before switching to another nest tree. Mean nest-tree fidelity was 4.2 (SE = 0.5) nights per nest tree. Individuals used a mean of 3.6 (SE = 0.6) nest trees per month, switching trees frequently. No differences were found in the nest-tree fidelity or use of trees by month for males and females (P = 0.273). A pregnant female collared in 2000 was an exception to the trend of switching trees frequently. Once she had her litter, she remained in the same nest tree for the remainder of the collar life (43 d). Prior to parturition, she switched nest trees regularly. No other females tracked were pregnant or had litters during the study.

Of the 59 nests we located, 41 (69%) were cavity nests and 18 (31%) were leaf nests. Despite nest boxes being available at most of the study sites, no collared flying squirrels were found in nest boxes during the study. Nest trees were found in forest ecotones between pure conifer and mixed northern hardwood-conifer stands comprised of red spruce, eastern hemlock, American beech and yellow birch. In these areas, there was a high abundance of snags of varying decay classes. At sites void of snags, such as Canaan Heights, flying squirrels tended to build leaf nests in conifers.

*Tree species.*—We found northern flying squirrel nests in 11 tree species: Norway spruce (n = 12), American beech (n = 10), yellow birch (n = 7), black birch (n = 6), Fraser magnolia (n = 6), black cherry (n = 5), red maple (n = 4), sugar maple (n = 3), red spruce (n = 3), yellow-poplar (*Liriodendron tulipifera*; n = 2) and cucumber magnolia (*Magnolia acuminata*; n = 1). The proportion of tree species used as nest trees differed significantly from the abundance of each species within the home range of individual flying squirrels ($G = 31.54$, $df = 12$, P = 0.003). Specifically, yellow birch and Fraser magnolia were used more than expected and striped maple, red maple and Norway spruce were used less than expected based on availability (Fig. 2).

*Cavity and land aspect.*—Virginia northern flying squirrels chose cavity nests differently than statistically expected with respect to land aspect ($G = 12.41$, $df = 3$, P = 0.004; Fig. 3). A higher proportion of flying squirrel nest trees were located on north-facing aspects than the other 3 cardinal directions. When examining cavity entrance aspect of the flying squirrel nest trees compared to the random tree aspects, selection was not statistically different ($G = 6.4$, $df = 3$, P = 0.240; Fig. 4).

*Nest tree characteristics.*—We found no statistical difference between the nest tree selection of male and female flying squirrels or between years (P = 0.177); therefore, data was pooled for analysis. Univariate analysis found that 10 of 24 nest-tree characteristics differed significantly from random trees (Table 1). Elevation, tree height, den height, nest tree DBH, average overstory height and average snag height were significantly greater than randomly selected trees (Table 1). Nest tree decay class, number of overstory trees surrounding the nest tree, percent of seedling cover and distance to nearest trail were significantly lower than randomly selected trees (Table 1).

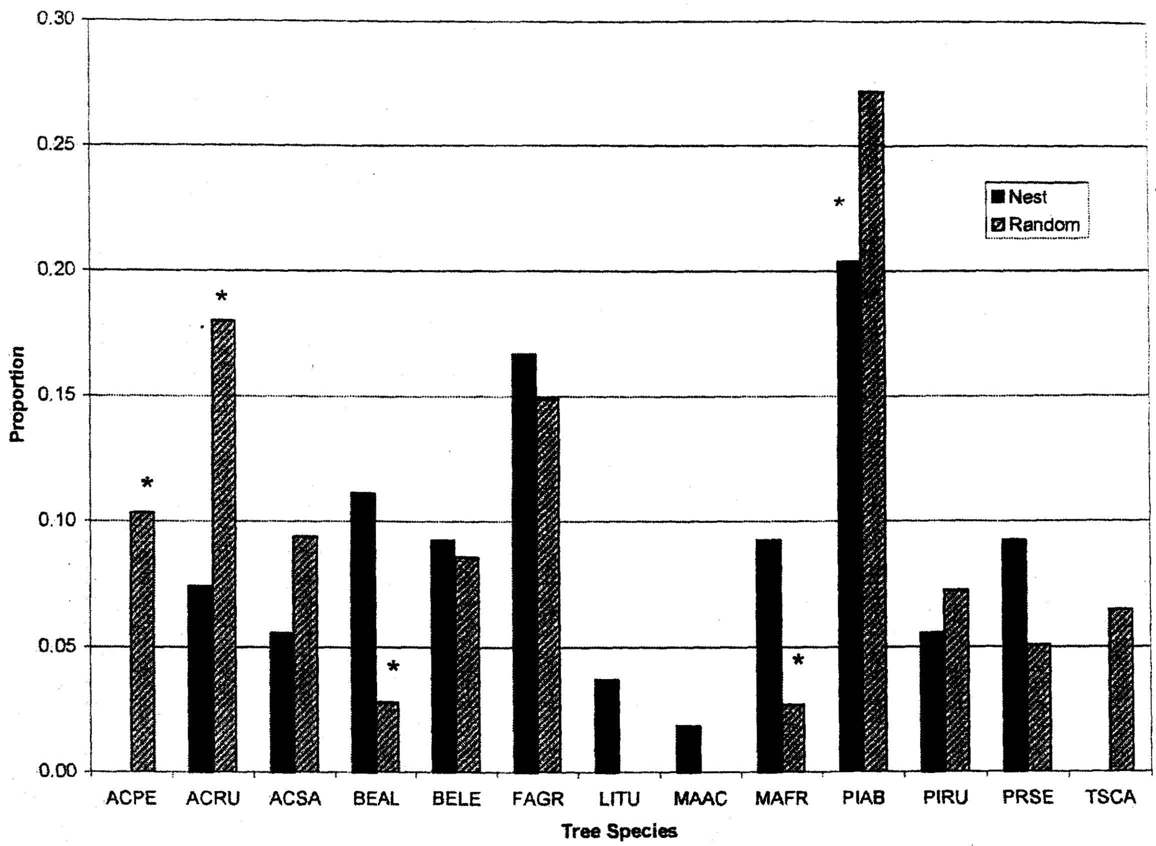


FIG. 2.—Proportion of nest-tree species used by Virginia northern flying squirrels (n = 59) during the summers of 2000 and 2001 compared with abundance of tree species (n = 59). Acronyms for tree species are as follows: ACPE—*Acer pensylvanicum*, ACRU—*Acer rubrum*, ACSA—*Acer saccharum*, BEAL—*Betula alleghaniensis*, BELE—*Betula lenta*, FAGR—*Fagus grandifolia*, LITU—*Liriodendron tulipifera*, MAAC—*Magnolia acuminata*, MAFR—*Magnolia fraseri*, PIAB—*Picea abies*, PIRU—*Picea rubens*, PRSE—*Prunus serotina*, TSCA—*Tisuga canadensis*. Asterisks indicate species where adjusted standardized residuals were >3.00

Univariate habitat analysis also found 11 of 24 tree characteristics differed between leaf nests and cavity nests (Table 2). Elevation, tree height, nest height, average DBH of the overstory, number of snags and the height of the snags were all significantly greater at leaf nests than at cavity nests (Table 2). Slope, decay class, midstory cover and rock cover were significantly less at leaf nests compared to cavity nests (Table 2). Because there were differences in the characteristics between leaf nests and cavity nests, we only used cavity nest trees in the logistic regression. We chose to report on the comparison between the nest trees (leaf and cavity) and random trees because it is unknown which variables are biologically significant and which are different for other non-biological reasons.

Logistic regression analysis identified three characteristics, nest tree DBH, average height of the overstory and nest tree height, that were successful in building a logistic model identifying Virginia northern flying squirrel cavity nest trees (Table 3). The logistic model had a predictive capability of $R^2 = 0.422$ in identifying Virginia northern flying squirrel cavity nest trees vs. random cavity trees. When the regression model was validated using a jackknife procedure, 57.4% of nest trees and 83.0% of random trees were classified correctly giving an overall correct classification of 70.2% (Table 4).

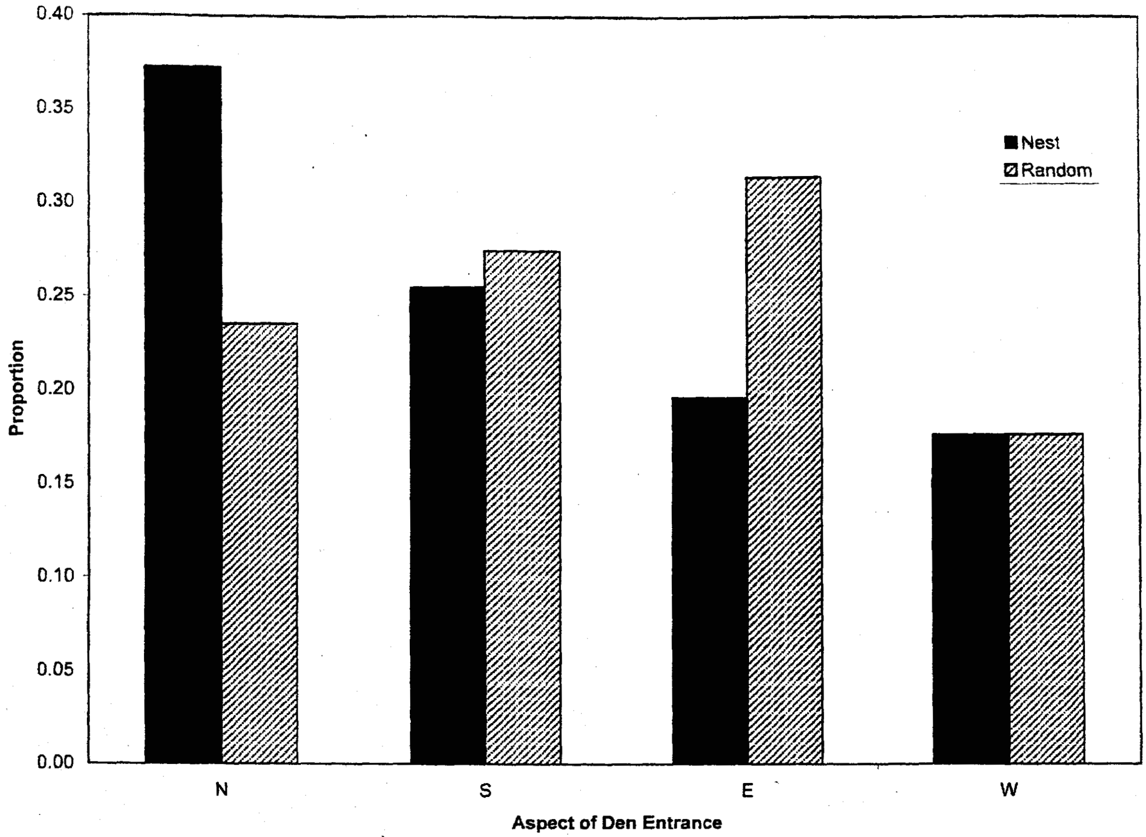


FIG. 3.—Proportion of den entrances of cavity trees (n = 41) used by Virginia northern flying squirrels during summer 2000 and 2001 found facing 4 aspects (north, south, east and west) compared with the entrance aspects of randomly located trees (n = 41) in West Virgina

## DISCUSSION

Virginia northern flying squirrels used both cavities and leaf nests during summer and fall. Weigl *et al.* (1999) reported the same general trend in North Carolina. Hackett and Pagels (2003) found squirrels using cavities, leaf nests and subterranean structures in Virginia. Carey *et al.* (1997) also found flying squirrels using both leaf and cavity nests during summer in the Pacific Northwest. Urban (1988), however, reported that Virginia northern flying squirrels in West Virginia exclusively used leaf nests. At that site (Stuart Knob), we found flying squirrels using cavity nests in a higher proportion than leaf nests. Therefore, our results again most closely match Weigl *et al.* (1999), Hackett and Pagels (2003) and Carey *et al.* (1997). One possible reason for the discrepancy between our findings and those of Urban (1988) may be the above average rainfall and below average temperatures that occurred during the first year of the study (NOAA Climate Archives, 2000). Northern flying squirrels may select cavities over leaf nests to reduce exposure to colder temperatures, rainfall and predators (Bowan, 1992). Additionally, the timespan between Urban's (1988) study and ours may have been long enough for forest maturation and the creation of cavities at the study site (*i.e.,* more cavities available).

Norway spruce was the most commonly used tree species for nests of Virginia northern flying squirrels; however, Norway spruce was not used more than expected based on its abundance at the study sites. The conversion to Norway spruce at Canaan Heights in the

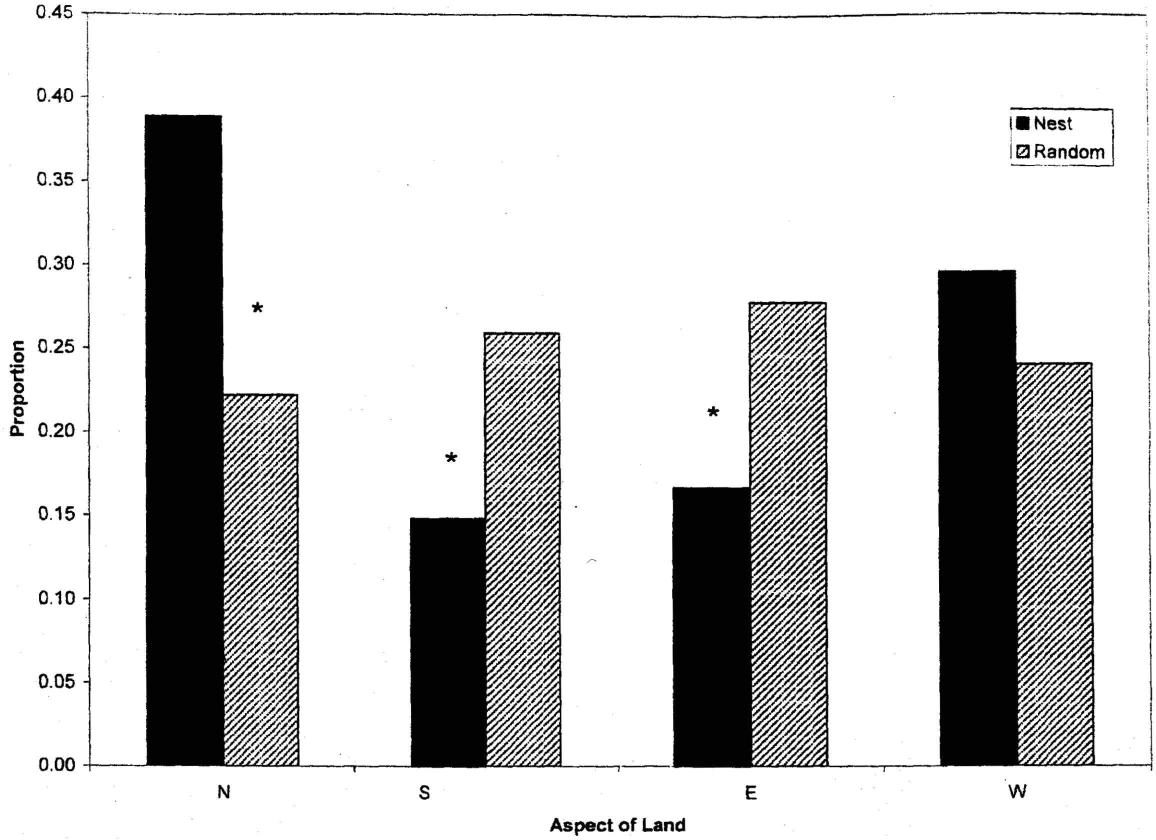


FIG. 4.—Proportion of nest trees (n = 59) used by Virginia northern flying squirrels during summer 2000 and 2001 found on four aspects of land (north, south, east and west) compared with the aspects of randomly located trees (n = 59) in West Virginia. Asterisks indicate aspects where adjusted standardized residuals were >5.00

early 1900s has produced a stand of large dominant overstory spruce. Perhaps northern flying squirrels were using Norway spruce as nesting sites at Canaan Heights because of its dominance and abundance in the overstory. Although non-native, the structural characteristics of the Norway spruce plantation may be a good representation of mature red spruce forests. Our results are similar to the results of Cotton and Parker (2000) in British Columbia in that large overstory conifers were used as nest trees in a higher proportion than deciduous species.

The next most common tree species used as nesting sites by Virginia northern flying squirrels were American beech and yellow and black birch and Fraser magnolia. These species have a high rate of decay, which provides a higher number of cavities (Carey, 1983; Wenger, 1984). Species that were not used as frequently such as oaks and sugar maple have a slower decay rate (Wenger, 1984), which reduces the number of cavities available for nesting. The wood of American beech and yellow and black birch and Fraser magnolia is also soft, which makes it easier for primary excavators to create cavities.

Virginia northern flying squirrels selected northern aspects for nesting sites. Similarly, Payne *et al.* (1989) found that in the southern Appalachians, Carolina northern flying squirrels typically selected nest trees on north facing slopes or in "coves." By selecting northerly aspects, perhaps squirrels are choosing nesting sites that receive less solar

TABLE 1.—Comparison of 24 characteristics between nest trees (n = 59) used by Virginia northern flying squirrels during the summers of 2000 and 2001 in West Virginia and randomly selected trees (n = 59)

| | Nest tree | | Randomly selected tree | | | |
|---|---|---|---|---|---|---|
| Variable | Mean | SE | Mean | SE | $Z$ | P[a] |
| Elevation (m) | 1114.3 | 40.2 | 1100.9 | 44.5 | 2.57 | 0.013 |
| Slope (%) | 14.9 | 1.2 | 13.8 | 1.9 | 0.57 | 0.570 |
| Decay class | 2.4 | 0.2 | 2.9 | 0.1 | −2.85 | 0.006 |
| Nest tree height (m) | 16.0 | 1.0 | 10.8 | 0.7 | 5.75 | 0.001 |
| Den height (m) | 9.2 | 0.8 | 5.4 | 0.4 | 4.69 | 0.001 |
| Nest tree DBH (cm) | 34.7 | 1.9 | 27.3 | 1.3 | 3.77 | 0.001 |
| Distance to nearest overstory tree (m) | 1.9 | 0.2 | 1.7 | 0.2 | 0.82 | 0.419 |
| Distance to nearest understory tree (m) | 2.6 | 0.5 | 1.9 | 0.2 | 1.34 | 0.187 |
| Number of overstory trees | 27.7 | 2.0 | 32.8 | 1.9 | −2.07 | 0.043 |
| Overstory basal area ($m^2$/ha) | 34.3 | 2.5 | 27.8 | 2.8 | 0.37 | 0.715 |
| Overstory mean DBH (cm) | 15.0 | 0.7 | 13.9 | 0.5 | 1.11 | 0.271 |
| Overstory mean height (m) | 13.8 | 0.6 | 9.1 | 0.3 | 6.55 | 0.001 |
| Number of snags | 5.1 | 0.7 | 4.1 | 0.5 | 1.42 | 0.161 |
| Average height of snags (m) | 8.1 | 0.6 | 6.1 | 0.5 | 3.05 | 0.004 |
| Snag basal area ($m^2$/ha) | 2.3 | 0.6 | 2.6 | 0.3 | −0.11 | 0.909 |
| Canopy closure (%) | 80.2 | 2.1 | 78.4 | 2.4 | 0.56 | 0.575 |
| Midstory cover | 9.6 | 1.4 | 12.1 | 1.6 | −1.29 | 0.202 |
| Seedling cover | 5.5 | 1.0 | 7.6 | 1.3 | −3.03 | 0.004 |
| Floor cover | 10.4 | 1.8 | 14.9 | 1.7 | 1.49 | 0.141 |
| Moss cover | 5.0 | 0.7 | 5.9 | 0.7 | −0.78 | 0.441 |
| Rock cover | 4.6 | 1.0 | 6.3 | 1.0 | −1.19 | 0.239 |
| Litter depth (cm) | 3.8 | 0.1 | 3.6 | 0.1 | 0.63 | 0.535 |
| Distance to nearest water (m) | 32.2 | 5.8 | 30.2 | 4.4 | 0.29 | 0.773 |
| Distance to nearest trail (m) | 13.0 | 3.1 | 25.6 | 4.1 | −2.96 | 0.005 |

[a] Wilcoxon test

radiation and are therefore cooler. This would be advantageous for a boreal species in West Virginia during warm months when temperatures can exceed 30 C. Additionally, conditions on northerly slopes and in coves are generally moist and thus facilitate a high rate of decay. Therefore, these locations could possibly have more cavities available than other aspects in the same general area. In addition, north facing slopes provide conditions suitable for fungi growth (Loeb *et al.*, 2000). The availability of fungi on these north-facing slopes may provide an important food source for flying squirrels (Mitchell, 2001; Pyare and Longland, 2002).

There has been one recent study published investigating the characteristics of nest trees of northern flying squirrels in the eastern United States (Hackett and Pagels, 2003). They found that Carolina northern flying squirrels used a variety of nest trees and generally chose larger and taller trees than what was available. Because of the importance of northern flying squirrels as a food source for the endangered northern spotted owl (*Strix occidentalis caurina*; Carey *et al.*, 1997), the remaining studies of nest tree characteristics have been conducted in the Pacific Northwest on other non-endangered subspecies of northern flying squirrel (Carey *et al.*, 1997; Cotton and Parker, 2000). Although a direct comparison is not possible due to the habitat differences between the Pacific Northwest and Appalachian Mountains, there are some similarities in the characteristics of nest trees selected by other subspecies of northern flying squirrel. For example, mean values of characteristics such as nest tree DBH,

TABLE 2.—Comparison of 24 characteristics of leaf nest trees (n = 18) and cavity nest trees (n = 41) used by Virginia northern flying squirrels during summer 2000 and 2001 in Randolph and Tucker counties, West Virginia

| | Leaf nest tree | | Cavity nest tree | | | |
|---|---|---|---|---|---|---|
| Variable | Mean | SE | Mean | SE | Z | P[a] |
| Elevation (m) | 1146.1 | 6.5 | 1103.7 | 6.1 | 3.52 | 0.001 |
| Slope (%) | 10.1 | 1.8 | 16.5 | 1.4 | −2.83 | 0.002 |
| Decay class | 1.5 | 0.2 | 2.7 | 0.2 | −3.49 | 0.001 |
| Nest tree height (m) | 21.1 | 1.1 | 14.3 | 1.1 | 3.10 | 0.001 |
| Den height (m) | 15.9 | 1.4 | 6.9 | 0.6 | 4.45 | 0.001 |
| Nest tree DBH (cm) | 35.5 | 3.0 | 34.5 | 2.3 | 0.61 | 0.272 |
| Distance to nearest overstory tree (m) | 2.2 | 0.3 | 1.8 | 0.2 | 1.36 | 0.088 |
| Distance to nearest understory tree (m) | 3.6 | 1.2 | 2.3 | 0.5 | 1.21 | 0.113 |
| Number of overstory trees | 26.6 | 3.8 | 28.0 | 2.4 | −0.12 | 0.451 |
| Overstory basal area ($m^2$/ha) | 36.7 | 3.1 | 32.0 | 2.8 | 1.05 | 0.147 |
| Overstory mean DBH (cm) | 17.4 | 1.2 | 14.2 | 0.9 | 2.13 | 0.017 |
| Average height of overstory (m) | 15.8 | 1.1 | 13.1 | 0.8 | 1.73 | 0.052 |
| Number of snags | 6.9 | 1.3 | 4.5 | 0.8 | 1.85 | 0.032 |
| Average height of snags (m) | 9.9 | 1.3 | 7.5 | 0.7 | 1.94 | 0.026 |
| Snag basal area ($m^2$/ha) | 2.7 | 0.5 | 2.4 | 0.3 | 1.11 | 0.133 |
| Canopy closure (%) | 81.0 | 3.9 | 80.0 | 2.5 | 0.00 | 0.500 |
| Midstory cover | 4.7 | 1.5 | 11.2 | 1.7 | −2.26 | 0.012 |
| Seedling cover | 4.9 | 1.4 | 5.7 | 1.3 | 0.01 | 0.496 |
| Floor cover | 20.4 | 4.7 | 13.0 | 1.7 | 1.24 | 0.107 |
| Moss cover | 4.9 | 1.1 | 5.0 | 0.9 | 0.00 | 0.500 |
| Rock cover | 1.4 | 1.1 | 5.6 | 0.2 | −2.68 | 0.004 |
| Litter depth (cm) | 1.2 | 0.3 | 1.6 | 0.2 | −1.59 | 0.055 |
| Distance to nearest water (m) | 45.3 | 13.9 | 27.8 | 6.1 | 1.62 | 0.053 |
| Distance to nearest trail (m) | 9.4 | 2.0 | 14.2 | 4.1 | 0.28 | 0.389 |

[a] Wilcoxon test

nest tree height and decay class were similar between our study and previous studies. Additionally, both regions showed a high variability in the characteristics of the nest trees used by flying squirrels. For example, Cotton and Parker (2000) indicated that the height, DBH and age of nest trees used by the squirrels they tracked were highly variable. Our results along with several other studies in the Pacific Northwest and Alaska (Mowrey and Zasada, 1984; Martin, 1994) found similar results. A high degree of plasticity in the nest tree selection of Virginia northern flying squirrels in conjunction with differences found

TABLE 3.—Logistical regression model of habitat variables surrounding Virginia northern flying squirrel cavity nest trees (n = 41) used in summer 2000 and 2001 and randomly located trees (n = 41) in Randolph and Tucker counties, West Virginia

| | Nest trees | | Random trees | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | Mean | SE | Mean | SE | Odds ratio | Estimate | SE | Chi-square | P |
| Intercept | | | | | | −3.8263 | 1.1843 | 10.43 | 0.001 |
| DBH (cm) | 33.9 | 1.74 | 28.2 | 1.54 | 0.802 | 0.2211 | 0.0904 | 5.98 | 0.015 |
| Average height of overstory (m) | 13.8 | 0.62 | 9.2 | 0.32 | 1.193 | 0.1769 | 0.0530 | 11.15 | 0.001 |
| Height of nest tree | 14.9 | 1.34 | 10.7 | 1.52 | 1.023 | 0.0232 | 0.0117 | 3.89 | 0.049 |

TABLE 4.—Validation of logistic regression of trees classified as nest or random based on a jackknife estimate

| Actual | Classified as | | % Correct |
|---|---|---|---|
| | Nest tree | Random tree | |
| Nest Tree (n = 41) | 23 | 18 | 57.4 |
| Random Tree (n = 41) | 7 | 34 | 83.0 |
| Total (n = 82) | 30 | 52 | 70.2 |

between nest trees located in managed and unmanaged forests indicate that northern flying squirrels may be less of a specialist in nest tree selection than previously thought (Hackett and Pagels, 2003).

Based on the high variability of nesting sites found in our study and the abundance of cavity trees in these habitats, availability of nesting sites does not appear to currently be a limiting factor for the Virginia northern flying squirrel. It is, however, important to continue to protect and enhance these habitat patches for this endangered species so nest sites will not become a limiting factor in the future. The retention of snags and larger older trees is important for providing nesting structures for both flying squirrels and other species such as cavity nesting birds and bats (Kunz, 1982; Aitken *et al.*, 2002). To ensure that adequate nesting structures are available in the future, it is crucial to promote some stand-level regeneration of species such as yellow birch. In the overstory, the creation of cavities in these trees will occur naturally and can also be accelerated by artificial means to provide nesting sites in areas with low cavity abundance (Carey, 1983).

Results from this study should fill in many knowledge gaps concerning the nesting ecology of the Virginia northern flying squirrel. This information should aid both researchers conducting future studies on this subspecies and forest managers developing management plans for sites inhabited by northern flying squirrels. Because many questions regarding Virginia northern flying squirrels remain unanswered, future research should focus on unexplored topics such as population dynamics and genetic isolation.

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## LITERATURE CITED

AITKEN, K. E. H., K. L. WIEBE AND K. MARTIN. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. *Auk,* **119**:391–402.

AUBRY, K. B. AND C. M. RALEY. 2002. Selection of nest and roost trees by pileated woodpeckers in coastal forests of Washington. *J. Wildl. Manage.,* **66**:392–406.

BAKER, R. H. 1983. Michigan mammals. Michigan State University Press, East Lansing. 642 p.

BAILEY, B. 1929. Mammals of Sherburne County, Minnesota. *J. Mammal.,* **10**:153–164.

BOWAN, M. S. 1992. Cold weather survival in the northern flying squirrel (*Glaucomys sabrinus*): a comparison of three species of sciurid. M.S. Thesis, Wake Forest University, Winston-Salem, North Carolina. 167 p.

CAREY, A. B. AND J. D. GILL. 1983. Direct habitat improvements—some recent advances, p. 80–87. *In:* J. W. Davis, G. A. Goodwin and R. A. Ockenfels (eds.). Snag habitat management: proceedings of the symposium. USDA Forest Service General Technical Report RM-99, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 226 p.

———, T. M. WILSON, C. C. MAGUIRE AND B. I. BISWELL. 1997. Dens of northern flying squirrels in the Pacific northwest. *J. Wildl. Manage.*, **61**:684–699.

———, J. KERSHNER, B. BISWELL AND L. DOMINGUEZ DE TOLEDO. 1998. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildl. Monogr.*, **142**:1–71.

COTTON, C. L. AND K. L. PARKER. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. *J. Mammal.*, **81**:1071–1086.

COWAN, I. MCT. 1936. Nesting habits of the flying squirrel, *Glaucomys sabrinus. J. Mammal.*, **17**:58–60.

FENNEMAN, N. M. 1938. Physiography of the eastern United States. McGraw-Hill, New York. 714 p.

HABERMAN, S. J. 1973. The analysis of residuals in cross-classified tables. *Biometrics*, **29**:205–220.

HACKETT, H. M. AND J. F. PAGELS. 2003. Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. *Am. Midl. Nat.*, **150**:321–331.

HAYES, R. L., C. SUMMERS AND W. SEITZ. 1981. Estimating wildlife habitat variables. USDA Fish and Wildlife Service. FWS/OBS-81/47. 111 p.

HOWELL, A. H. 1918. Revisions of the American flying squirrels. *N. Amer. Fauna*, **44**:1–64.

JACKSON, H. H. T. 1961. Mammals of Wisconsin. University of Wisconsin Press, Madison. 504 p.

KITTREDGE, J. 1928. Can the flying squirrel count? *J. Mammal.*, **9**:251–252.

KUNZ, T. H. 1982. Ecology of bats. Plenum Press, New York. 425 p.

LOEB, S. C., F. H. TAINTER AND E. CAZARES. 2000. Habitat associations of hypogeous fungi in the southern Appalachians: implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *Am. Midl. Nat.*, **144**:286–296.

MARTIN, K. J. 1994. Movements and habitat characteristics of northern flying squirrels in the central Oregon Cascades. M.S. Thesis, Oregon State University, Corvallis. 65 p.

MENZEL, M. A., T. C. CARTER, B. R. CHAPMAN AND J. LAERM. 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). *Can. J. Zool.*, **76**:630–634.

MENZEL, J. M., W. M. FORD, J. W. EDWARDS AND M. A. MENZEL. In Review. Homerange and habitat use of the endangered Virginia northern flying squirrel in the Central Appalachians. Wildlife Society Bulletin.

MERRITT, J. F., D. A. ZEGERS AND L. R. ROSE. 2001. Seasonal thermogenesis of southern flying squirrels (*Glaucomys volans*). *J. Mammal.*, **82**:51–64.

MITCHELL, D. 2001. Spring and fall diet of the endangered West Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*). *Am. Midl. Nat.*, **146**:429–443.

MOWREY, R. A. AND J. C. ZASADA. 1982. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management, p. 351–356. *In:* W. R. Meehan, T. R. Merrell, Jr. and T. A. Hanley (eds.). Fish and wildlife relationships in old growth forests: proceedings of a symposium. Bookmasters, Ashland, Ohio. 425 p.

NOAA CLIMATE ARCHIVES. 2000. http://www.lwf.ncdc.noaa.gov

PAYNE, J. L., D. R. YOUNG AND J. F. PAGELS. 1989. Plant community characteristics associated with the endangered northern flying squirrel, *Glaucomys sabrinus*, in the southern Appalachians. *Am. Midl. Nat.*, **121**:285–292.

PYARE, S. AND W. S. LONGLAND. 2002. Patters of ectomycorrhizal-fungi consumption by small mammals in remnant old growth forests of the Sierra Nevada. *J. Mammal.*, **82**:681–689.

SAS INSTITUTE, INC. 1990. SAS/STAT User's Guide. Version 6, 4th ed, Vol. 2. SAS Institute, Inc., Cary, North Carolina. 1028 p.

SOKAL, R. R. AND F. J. ROHLF. 1987. An introduction to the study of biostatistics. W. H. Freeman and Company, New York, New York. 363 p.

STAPP, P. 1992. Energetic influences on the life history of *Glaucomys volans. J. Mammal.*, **73**:914–920.

———, P. J. PEKINS AND W. W. MAUTZ. 1991. Winter energy expenditure and the distribution of southern flying squirrels. *Can. J. Zool.*, **69**:2548–2555.

STEPHENSON, S. L. 1993. Upland forests of West Virginia. McClain Printing Co., Parsons, West Virginia. 295 p.

STIHLER, C. W., J. L. WALLACE, E. D. MICHAEL AND H. PAWELCZYK. 1995. Range of (*Glaucomys sabrinus fuscus*), a federally endangered subspecies of the northern flying squirrel in West Virginia. *Proc. WV Acad. Sci.*, **67**:13–20.

STRAUSBAUGH, P. D. AND E. L. CORE. 1978. Flora of West Virginia. Seneca Books, Morgantown, West Virginia. 675 p.

URBAN, V. 1988. Home range, habitat utilization and activity of the endangered northern flying squirrel. M.S. Thesis, West Virginia University, Morgantown, West Virginia. 79 p.

U. S. FISH AND WILDLIFE SERVICE. 1985. Final rule for listing Carolina northern flying squirrel and Virginia northern flying squirrel as endangered. 50 FR 27002; July 1, 1985.

———. 1990. Appalachian northern flying squirrel (*Glaucomys sabrinus fuscus* and *Glaucomys sabrinus coloratus*) recovery plan. Newton Corner, Massachusetts. 53 p.

VORA, R. S. 1988. A comparison of the spherical densiometer and ocular methods of estimating canopy cover. *Great Basin Nat.*, **48**:224–227.

WEIGL, P. D. 1978. Resource overlap, interspecific interactions and the distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*. *Am. Midl. Nat.*, **100**:83–96.

——— AND D. W. OSGOOD. 1974. Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. *Am. Midl. Nat.*, **92**:482–486.

———, T. W. KNOWLES AND A. C. BOYNTON. 1999. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. North Carolina Wildlife Resources Commission, Raleigh, North Carolina. 140 p.

WELLS-GOSLING, N. AND L. R. HEANEY. 1984. *Glaucomys sabrinus*. *Mammal. Species*, **229**:1–8.

WENGER, K. F. 1984. Forestry handbook. John Wiley & Sons, New York. 1335 p.

WITT, J. W. 1992. Home range and density estimates for the northern flying squirrel, *Glaucomys sabrinus*, in western Oregon. *J. Mammal.*, **73**:921–929.

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