

**HABITAT ASSOCIATIONS BETWEEN THE NORTHERN FLYING
SQUIRREL AND RED SPRUCE**

by

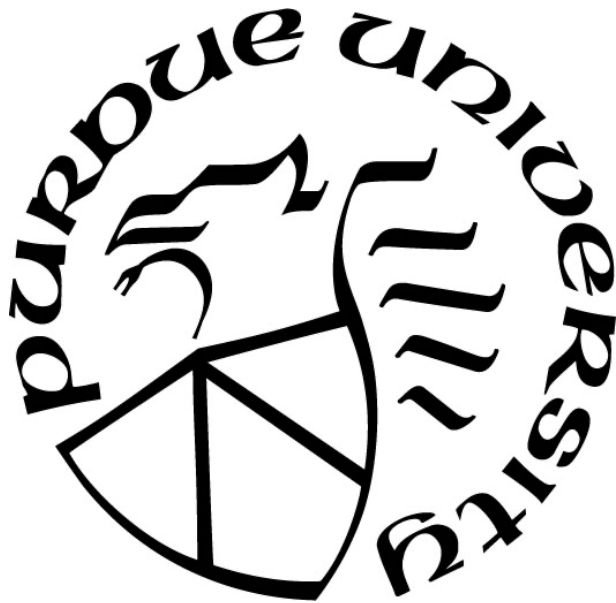
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Dedicated to my family, for all their love and support.

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ABSTRACT

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Title: Habitat Associations Between the Northern Flying Squirrel and Red Spruce

Major Professor: Elizabeth A. Flaherty

Red spruce forests, one of the most critically endangered ecosystems in the United States provides critical habitat for several endemic species or subspecies of the Appalachian Mountains, including the Virginia northern flying squirrel. Once listed as threatened under the Endangered Species Act, the Virginia northern flying squirrel was delisted in 2013. Managers are currently focusing their efforts on projects that increase the extent and connectivity of the squirrel's habitat through red spruce restoration. At present, there is a paucity of available data to assess the implications of the silvicultural activities associated with red spruce restoration on the movement and occupancy of the Virginia northern flying squirrel. In order to inform management activities, I measured home range, fine-scale habitat use, and estimated detection and occupancy for northern flying squirrels across a gradient of red spruce stands in the Monongahela National Forest. I concluded that home ranges for northern flying squirrels within this region are comprised primarily of red spruce and that northern flying squirrels were selecting larger diameter trees compared to the nearest available neighbor. Additionally, I found that microhabitat characteristics alone did not sufficiently predict northern flying squirrel occupancy and that acoustic methods for surveying northern flying squirrels will require further refinement. Future research efforts should focus on a combination of landscape-level and microhabitat covariates to best predict occupancy of this species across the landscape. Future red spruce management should be approached with caution

regarding the potential impact on northern flying squirrel habitat in the short-term. I recommended using spatially-explicit modeling to assess the long-term effects of proposed red spruce restoration projects on northern flying squirrel population demographics, dispersal, and metapopulation connectivity prior to the implementation of silvicultural treatments.

CHAPTER 1. INTRODUCTION

1.1 Introduction

This research examined habitat associations between the northern flying squirrel (*Glaucomys sabrinus fuscus*) and red spruce (*Picea rubens*) in the Monongahela National Forest (MNF), West Virginia. The Virginia northern flying squirrel is a small, arboreal rodent found in high elevation spruce-fir forests of the Appalachian Mountains including within the MNF. Red spruce is a shade tolerant, montane conifer that once dominated forests in this region. However, red spruce has experienced a decline of its historic range by >90% in West Virginia from timber harvest and subsequent alteration of the soil from slash burning (Rentch et al. 2010). Red spruce forests, which provide critical habitat for several endemic species or subspecies of this region, are one of the most critically endangered ecosystems in the United States (Noss et al. 1995).

The US Fish and Wildlife Service (USFWS) listed Virginia northern flying squirrel on the 1973 Endangered Species Act in 1985 amid concerns of low population size. For the next 30 years, northern flying squirrel occupancy on public lands heavily restricted management activities. After delisting of the squirrel in 2013, managers focused habitat efforts on increasing connectivity and extent of the squirrel's habitat through red spruce restoration projects. Current management practices aim to accelerate red spruce recovery through natural succession trajectories by using selective harvest techniques, such as thinning, to release suppressed mid-to-understory red spruce (USDA 2006). However, thinning initially disturbs available flying squirrel habitat by reducing already limited characteristics of structural diversity within the canopy and midstory in second-growth stands (McGee et al. 1999; Holloway and Malcolm 2006). Because of this, managers must balance the trade-offs between the long-term benefit of restoration of red spruce ecosystems with the short-term costs associated with habitat disturbance from forest management.

Researchers have primarily modeled northern flying squirrel habitat in the Appalachian region with coarse-grained landscape features to identify areas of high conservation priority (Odom et al. 2001; Menzel et al. 2006). At the stand level, red spruce is a key predictor of northern flying squirrel occupancy (Payne et al. 1989; Ford et al. 2004; Holloway and Malcolm 2006). However, the northern flying squirrel exists at low densities across the landscape. There is a crucial need for managers to probabilistically relate forest structural elements, (i.e., microhabitat), with flying squirrel occupancy (Ford et al. 2004).

At present, there is a paucity of available data on Virginia northern flying squirrel movement and occupancy to assess the implications associated with the restoration of red spruce. My primary research objectives were to measure home range size and to relate flying squirrel occupancy to fine-scale habitat use prior to red spruce restoration. These data will serve as baseline information to allow managers to assess current habitat conditions and monitor changes in habitat use by northern flying squirrels following timber management.

I monitored collared northern flying squirrels using radio telemetry to record nightly locations and diurnal den trees to estimate home range size. I described microhabitat conditions surrounding nest trees and available trees to determine which features northern flying squirrels preferentially selected within a forested stand. I then used acoustic monitors and microhabitat surveys at monitoring sites to estimate occupancy and habitat use of northern flying squirrels across red spruce gradients in the Monongahela National Forest. I compared my occupancy results to a species-specific coarse-scale habitat model to help managers determine areas of conservation priority (Menzel et al. 2006).

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CHAPTER 2. NORTHERN FLYING SQUIRREL HOME RANGE AND DEN SITE CHARACTERISTICS

2.1 Introduction

Over the last 30 years, a primary focus of the US Forest Service has been to invest management resources to restoring threatened ecosystems such as hardwoods in the Alluvial Valley, shortleaf pine (*Pinus echinata*) in the Ozark highlands, longleaf pine (*Pinus palustris*) in the Gulf Coastal Plains, and red spruce (*Picea rubens*) in the Allegheny mountains of West Virginia (Stanturf et al. 2001; Rentch et al. 2007). The restoration of red spruce became a priority in 2006 with the creation of a separate management prescription document for spruce dominated forests by the U.S Forest Service (U.S Forest Service 2006; Gundy et al. 2012). Red spruce, also commonly called West Virginia spruce, is a temperate, shade tolerant conifer of the eastern United States and Canada that is highly valued for timber production (Blum 1990). Presently, within the Appalachian Mountains, less than 15% of the historical range is comprised primarily of red spruce, and the total remaining area of red spruce forest in this region is $< 300 \text{ km}^2$ (Adams and Stephenson 1989; Schuler et al. 2002).

Large, landscape-level forest disturbance began in the Allegheny Mountains with the conversion of spruce-fir forest to agricultural land by European colonists in the early 1800s. Prior to this disturbance, red spruce comprised approximately 50% of the mixed conifer overstory within the region (Mayfield and Hicks 1995; Rentch et al. 2010). By 1920, widespread commercial timber harvest reduced the range of red spruce by 90% in West Virginia, leaving functionally isolated patches at high elevations (Rentch et al. 2010). Subsequent burning of the remaining slash altered the soil composition and destroyed the seed bank, thereby reducing or preventing natural regeneration (Allard and Leonard 1952). Red spruce forests are therefore considered one of the

most critically endangered ecosystems in the United States (Noss et al. 1995). Not only are the forests themselves rare, they also provide critical habitat for threatened and endangered endemic species of this region, such as the cheat mountain salamander (*Plethodon nettingi*) and the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*).

The Virginia northern flying squirrel, one of two subspecies found in the Allegheny Mountains of the central Appalachians, is a forest obligate, typically associated with high-elevation spruce-fir forests dominated by red spruce, eastern hemlock (*Tsuga canadensis*), and the adjacent ecotones (Loeb et al. 2000; Mitchell 2001; Arbogast 2007; Smith et al. 2011). Whereas observations indicate the presence of Virginia northern flying squirrel in a diverse range of stand conditions and age classes, mature red spruce stands with a high density of large diameter trees, abundant snags, downed coarse woody debris, and the presence of both hypogaeal fungi and lichens are optimal (Ford and Rodrigue 2007; Trapp et al. 2017). Documentation in the past 30 years of the Virginia northern flying squirrel confirms species in seven West Virginia counties, however, its range is primarily restricted to the Monongahela National Forest and a small portion of the adjacent George Washington National Forest in Virginia (Stihler et al. 1995; Ford and Rodrigue 2007).

In 1985, amid concerns of low population size, the US Fish and Wildlife Service (USFWS) listed Virginia northern flying squirrel on the 1973 Endangered Species Act, and for the next several decades, the presence of the flying squirrel on private and public land heavily restricted management and commercial activities. After modeling population dynamics and a review of their status, the USFWS delisted Virginia northern flying squirrel in 2013 (USFWS 2013). Currently, the Virginia northern flying squirrel is a driver of many red spruce restoration projects that include management objectives for increasing connectivity and extent of the squirrel's habitat. Managers

primarily use selective silvicultural techniques to open canopy gaps, and release suppressed mid-to-understory red spruce to accelerate recovery through natural succession trajectories (Rentch et al. 2016). Thinning techniques used in canopy-gap formation remove all standing, live trees with irregular branching, structural deformities, and rot near suppressed understory red spruce saplings, which may serve as northern flying squirrel dens (Carey et al. 1997). Thinning, at least in the short term, disturbs available habitat by reducing the density of conifers, snags, canopy cover, hypogeous mycorrhizal fungi and coarse woody debris, which provides structural diversity that is often already limited in second-growth stands (McGee et al. 1999; Holloway and Malcolm 2006).

However, red spruce is gradually recovering from historical timber harvest practices without active intervention from natural resource managers. Analysis of approximately 40 years of aerial photographs in Tucker County, West Virginia, demonstrated an increase in red spruce within the canopy (Fortney and Rentch 2003). Understory red spruce saplings and seedlings in multiple hardwood-spruce ecotones across the state of West Virginia increased in conjunction with either stable or declining understory hardwood densities (Rollins et al. 2010). Furthermore, Rentch et al. (2010) projected that red spruce will fill approximately 40% of all canopy gaps formed in hardwood dominated tree stands with red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis* var. *alleghaniensis*) in the Monongahela National Forest and nearby Kumbrabow State Forest. Concerns remain over trade-offs between the short-term costs of habitat loss and disturbance from forest management and the long-term benefit of restoration of a red spruce ecosystem. Presently, there is a lack of data related to Virginia northern flying squirrel population size, movement and persistence to evaluate the implications associated with red spruce restoration. Therefore, my primary research objective was to measure habitat use prior to red spruce restoration with a focus on estimating fine-scale habitat use, home

range size, vegetation characteristics within home ranges, and den site use using radio telemetry methods. These data serve as baseline information to evaluate habitat use in existing habitat conditions as well as after timber management, allowing managers to monitor changes in habitat use by northern flying squirrels.

2.1.1 Study Area

Red spruce heavily dominated the canopy with understory cover comprised of black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), red maple, and yellow birch. Less predominant species in the canopy included eastern hemlock, sweet birch (*Betula lenta*), striped maple (*Acer pensylvanicum*), and red oak (*Quercus rubra*). Though the understory cover was sparse, understory shrub species included great rhododendron (*Rhododendron maximum*), velvetleaf blueberry (*Vaccinium myrtilloides*), and northern lowbush blueberry (*Vaccinium angustifolium*) with the forest floor covered in liverwort (*Bazzania triobata*; Stephenson and Clovis 1983). Both sites were second-growth stands and experienced timber harvest at least once in the past century. Currently, the USDA Forest Service manages the surrounding area for open habitats, including even-age timber harvest (<10 years), recreational trails, skidder trails, and roads.

I focused trapping efforts in two designated management areas in the Monongahela National Forest (MNF), West Virginia, USA prior to red spruce restoration activities. These stands were approximately 10 ha, comprised of mixed hardwoods and conifers located in Randolph County (Lat. -38.685833°, Long 79.5986°) with an elevation of 1200 m. Steep slopes, narrow valleys running from north-east to south-west, and broad ridges of the Allegheny Mountains and Plateau sub-physiographic region of the Appalachian Mountains characterize the site (Fenneman 1938; Byers et al. 2010). Climatic conditions are typically cool and wet with frequent fog. The annual average temperature ranges from 6.7–9.4° C, with the possibility of freezing temperatures year-

round (Stephenson 1993). The annual precipitation ranges from 120–150 cm throughout the year and this region experiences an average of ≥ 300 cm of annual snowfall (Rentch et al. 2007).

2.2 Methods

I installed 40 Tomahawk live traps (No. 201; 14 x 14 x 41 cm, Tomahawk Live Trap Co., Hazlehurst, WI, USA) at the first field site within the Spruce Mountain Grouse Management Area in April 2019, and 40 traps at the second field site within the Grassy Mountain Timber stand improvement area in June 2019. I covered traps in tarp to provide protection against the elements. I set multiple transects at each site spaced 50 m apart. I set traps within each transect spaced 50 m apart and attached traps 1.5 m above the ground on the bole of a tree similar to the method described by Carey et al. (1991). I baited traps with apples as a source of water and a mixture of rolled oats, peanut butter and molasses (Waters and Zabel 1995; Smith and Nichols 2003).

I checked traps at dawn, closed them, and reopened them at dusk to reduce risk of capture of diurnal non-target species such as red squirrels (*Tamiasciurus hudsonicus*). For every adult flying squirrel captured, I inserted an individually sterilized HPT9 PIT-tag (Biomark, Boise, ID, USA) for individual identification and fit a 3.1 g ATS M1530 mini cable-tie mammal radio collar (Advanced Telemetry Systems, Isanti, MN, USA). I recorded age, sex, reproductive condition and mass of all individuals captured. I performed trapping activities under a permit from the West Virginia Department of Natural Resources, Wildlife Resources Section (2019.113). My live-trapping methods followed guidelines from the American Society of Mammalogists (Sikes et al. 2016) and Institutional Animal Care and Use Committee at Purdue University (PACUC) approved all methods involving live vertebrates (PACUC #1309000931).

I monitored collared squirrels every evening using handheld receivers (R-1000, Telonics, Inc., Meza, Arizona) and a flexible H-antenna (RA-23K VHF, Telonics, Inc., Meza, Arizona).

When weather permitted, I obtained locations once per night from June to August 2019 from squirrels using close range biangulation (<0.4 km) from dusk until squirrel activity slowed (usually 2–3 hr after sunset). I located den sites in individual trees during diurnal telemetry sessions using homing methods and confirmed that the stationary location was not due to an alternative event such as mortality or a dropped collar.

Upon locating a den site, I flagged the tree, assigned it a unique identification number, and recorded the GPS location. I collected vegetation data when the den site was unoccupied to prevent the flying squirrel from abandoning the den (Carey et al. 1997). I described the microhabitat conditions surrounding the nest tree and available trees according to the methods described in Bakker and Hastings (2002) by sampling a 0.1 ha plot around each nest tree to characterize microhabitat and available trees. Available trees included any tree within the 0.1 ha plot with a DBH > 10 cm. I conducted a paired t-test average for diameter at breast height (DBH) and average lowest living branch of the nest trees and available trees. I generated location data points from telemetry bearing data using the best biangulation estimator in LOAS (location of a signal, Ecological Software Solutions LLC, California, USA, Koprowski et al. 2008). I examined the locations from each squirrel and determined whether those locations were within the Grassy Mountain red spruce stand using ArcGIS Pro 10.2 (ArcGIS Pro 10.2, Esri, California, USA). I estimated home range with evening and den site locations using a 100% and 50% minimum convex polygon (MCP) using the minimum bounding geometry data management tool in ArcGIS Pro 10.2. I calculated the size of the home range overlap between individuals using adehabitatHR package in program R version 3.6.2 (Calenge 2006; R Core Team 2017). I calculated percent home range overlap using the equation and methods described in Bernstein et al. (2007).

2.3 Results

I captured, radio-collared, and released 8 adult northern flying squirrels including 7 males and 1 female within the Grassy Mountain timber stand improvement unit. I tracked squirrels for approximately 1 month and I collected an average of 10.7 locations for each squirrel. I estimated that an average of 72.0% of an individual's locations were within the red spruce stand (Table 2.1). The mean (\pm SE) home range size for the 7 males was 12.8 ± 6.1 ha and the home range of the only female was 4.8 ha (Table 2.1). The mean home range overlap for all individuals, regardless of sex, was 2.5 ± 1.9 ha. The mean home range overlap between males was 2.5 ± 2.2 ha, whereas the overlap between males and the only female was 2.6 ± 1.2 ha (Table 2.2). The average percent overlap for all 7 home ranges (\pm SD) was $16.1 \pm 12.7\%$, percent overlap between males was $12.9 \pm 11.7\%$, whereas percent overlap between males and the only female was $24.1 \pm 12.2\%$ (Table 2.2).

I located 12 nest trees for 7 individuals in 4 species of trees, black cherry, red maple (*Acer rubrum*), sugar maple, and red spruce. All den site locations were within cavities in living trees, I did not observe nesting in snags. I identified at least 1 nest site for each individual squirrel during the month I recorded telemetry locations, with several individuals having multiple nest sites. Red spruce was the most commonly used nest tree (n=4) followed closely by black cherry (n=3). The smallest nest tree was a red spruce with a DBH of 27.5 cm and the largest nest tree was a black cherry with a DBH of 82.4 cm. The mean (\pm SD) DBH of nest trees was 42.5 ± 15.7 cm, the mean total height of the tree was 21.9 ± 2.0 m, and the mean height of the lowest living branch was 9.4 ± 3.1 m (Table 2.3). Available trees had a mean DBH of 27.4 ± 4.8 cm and a mean lowest living branch height of 9.4 ± 1.5 m (Table 2.3). A paired t-test comparing the average DBH between the nest trees and available trees indicated a significant difference ($t_{0.05(2)10} = 3.30$, $p = 0.004$). Results

from a paired t-test comparing average lowest living branch height between nest trees and available trees was not significant ($t_{0.05(2)10} = -0.015$, $p = 0.49$).

2.4 Discussion

Spruce is a key habitat element in the eastern United States and is a key predictor of northern flying squirrel presence on the landscape (Payne et al. 1989; Ford et al. 2004; Holloway and Malcolm 2006; Menzel et al. 2006). I found that the majority (mean 72%) of locations were within red spruce stands. One male (4A87) had 90.9% of all telemetry locations within the red spruce stand. Diggins and Ford (2017) similarly found northern flying squirrels had a large percentage of locations within stands with a dominant conifer overstory for adult flying squirrels in Pocahontas and Randolph Counties, WV. They found that 73.5% of all telemetry points were located in a stand with a conifer dominant overstory and of the telemetry points within a dominant hardwood overstory, at least 69.6% had a partial overstory composition of conifers (Diggins and Ford 2017). Diggins and Ford (2017) concluded that the presence of red spruce, or a similar conifer surrogate, was more important when predicting Virginia northern flying squirrel microhabitat selection than other habitat features.

My home range estimates fell within previously reported values for both males and females in West Virginia and across the entirety of ranges of the northern flying squirrel (Table 2.4). I estimated an average home range size of 12.8 ha for males, which was larger than the values reported in West Virginia by Urban (1988) of 5.2 ha and Diggins and Ford (2017) of 5.8 ha during the summer and early fall months. My home range estimate for the only female of 4.8 ha was smaller than home ranges previously reported in West Virginia but similar to those reported in Virginia, North Carolina and Tennessee (Table 2.4). The largest home range estimated in my study was 41.3 ha. However, this individual was a male that moved to a nearby spruce stand immediately

after capture, returned to the initial capture site 3 days later, and then remained there for the duration of the study. This large home range was most likely a response to disturbance and not a true representation of his actual home range. However, Menzel et al. (2006) reported the largest home range size for male northern flying squirrels in West Virginia of 59.8 ha.

I did not observe significant home range overlap amongst males or between the sexes, whereas previous research concluded that average percent overlap between females was greater than between the sexes or amongst the males. This is likely due to my sample size of one collared female. This female was reproductively active and showed signs of lactation. I observed an average of 16% overlap between all individuals, which was lower than previously reported for northern flying squirrels. However, I conducted my study during the summer months when females may be less tolerant of home range overlap while rearing kits and when nesting communally is not essential for energy conservation (Stapp et al. 1991). I only recorded locations for 1 female and therefore were unable to determine percent overlap amongst females. Smith et al. (2011) estimated that home range overlap between female and male dyads ($n=5$), and amongst male dyads ($n=2$) was approximately 45%. Researchers have observed similar percent overlap in home ranges in southern flying squirrels (*Glaucomys volans*) during the summer months. Jacques et al. (2017) reported that female southern flying squirrel home ranges overlapped with males approximately 24.1% and there was 12.5% overlap between male home ranges. All the individuals in this study overlapped with the other 6 individuals; I did not observe any independent home ranges (Figure 2.1). In contrast, Smith et al. (2011) reported only 40% of female northern flying squirrels had a home range that overlapped with another individual. Northern flying squirrels inhabit areas with stands of large trees, which on the forest landscape are increasingly fragmented and rare due to the historical and present forestry practices. Hence, overlap may be due to limited dispersal

opportunities as opposed to sociality or lack of territoriality in the northern flying squirrel (Smith et al. 2011). Increased home range overlap due to limited dispersal opportunities is not unique to northern flying squirrels. Waters et al. (1994) found that in fragmented forests with a large conifer component, similar to those found in West Virginia, Eurasian red squirrels (*Sciurus vulgaris*) home range size and space use strongly relates to the patch structure and the presence of hedgerows, which serve as a corridor for dispersing juveniles.

When I compared the average DBH between nest trees and available trees, I reported a significant difference, suggesting that the squirrels are selecting for large trees with a greater DBH than those trees surrounding the dens. Cotton and Parker (2000) and Pyare et al. (2010) also concluded that northern flying squirrels preferred larger, older, taller nest trees than randomly available trees. I observed only internally located dens in living trees. I did not observe any drays or snags as nesting locations. On Prince of Wales Island, AK, 42% of the den sites for northern flying squirrels were in live trees with no sign of an external dray, however 51% of these nests were in snags. (Pyare et al. 2010). Although there have been reports of multiple individuals sharing a single den, I did not observe any instances of this. I conducted my study during the summer months and den sharing may be more likely in my study area when individuals are thermally stressed in the winter months (Carey et al. 1997).

2.5 Management Implications

My study suggests that Virginia northern flying squirrels home ranges in this area are primarily located within red spruce forests, and that they are preferentially selecting large diameter trees for nesting. The estimated home range size and overlap is suggestive of limited available habitat and low opportunities to disperse across the forest matrix. Previous research on the response of northern flying squirrels to thinning and similar silvicultural treatments have reported

negative effects on squirrel densities (Holloway and Smith 2011; Manning et al. 2012). Density of conifers, especially spruce, canopy cover, hypogeal fungi and snags are all key northern flying squirrel microhabitat site characteristics. These microhabitat characteristics are significantly impacted during and after canopy-gap thinning treatments, which may lead to a potential decrease in population density on harvested sites (Holloway and Malcolm 2006; 2007). Given the high association of the Virginia northern flying squirrel with red spruce stands, the evidence of gradual, natural red spruce recovery, and low-density occurrence of this squirrel on the landscape, I recommend caution regarding the use of small-scale silvicultural treatment in remnant spruce stands. While it is likely that red spruce management will benefit northern flying squirrels long-term, I recommend assessing the effects of proposed silvicultural treatments on dispersal, metapopulation connectivity, and population dynamics using spatially explicit modeling that incorporates local habitat factors and the local landscape in addition to ecological parameters specific to northern flying squirrels (Trapp et al. 2019).

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Table 2.1 Northern flying squirrel live-capture data, telemetry data and home range estimates for 7 flying squirrels

Home range size (ha) of adult northern flying squirrels (*Glaucomys sabrinus fuscus*) using minimum convex polygons in Randolph County, West Virginia during the summer of 2019.

Sex	ID	Initial capture date	Number of locations	Locations in red spruce (%)	Minimum convex polygon (MCP) (ha)	
					100 %	50 %
F	2320*	23 Jun 2019	13	84.6	4.8	1.2
M	4838	14 Jun 2019	12	58.3	17.4	1.1
M	F839	26 Jun 2019	10	60.0	41.3	1.6
M	4A29	22 Jun 2019	8	87.5	5.0	0.2
M	F6E2	22 Jun 2019	11	90.9	6.8	0.4
M	F632	23 Jun 2019	10	72.7	3.5	0.6
M	4A87	23 Jun 2019	11	50.0	2.7	0.1

Table 2.2 Home range overlap percent and size estimates

Minimum convex polygon overlap \pm SD (ha) and percentage overlap \pm SD in *Glaucomys sabrinus* fuscus home ranges between all individuals and by sex in Randolph County, West Virginia during the summer 2019 field season. The only adult female is denoted with an asterisk.

Individual	Average overlap (ha)	Average percent overlap (%)
4838	3.5 \pm 3.0	13.3 \pm 4.5
2320*	2.6 \pm 1.1	24.1 \pm 12.2
F839	4.5 \pm 2.5	10.0 \pm 4.8
4A29	2.2 \pm 1.0	22.0 \pm 18.4
F6E2	1.7 \pm 1.3	10.7 \pm 6.9
F632	2.0 \pm 0.9	22.7 \pm 19.0
4A87	1.2 \pm 1.0	9.9 \pm 6.0
Totals		
Male/male	2.5 \pm 2.2	12.9 \pm 11.7
Male/female	2.6 \pm 1.2	24.1 \pm 12.2
All individuals (n=7)	2.5 \pm 1.9	16.1 \pm 12.7

Table 2.3 Nest tree characteristic for northern flying squirrels

Characteristics of nest trees \pm SD (n =12) and available trees \pm SD sampled in a 0.1 ha plot for adult northern flying squirrels (*Glaucomys sabrinus fuscus*) in Randolph County, West Virginia. I measured characteristics at the level of the nest tree and the surrounding local habitat.

Characteristic	
Nest tree	
Average height (m)	21.9 ± 2.0
Average dbh (cm)	42.5 ± 15.7
Average lowest branch height (m)	9.4 ± 3.1
Local	
Average dbh (cm)	27.4 ± 4.8
Average lowest branch height (m)	9.4 ± 1.5
Average canopy cover	89.6 ± 5.3
Snag density (per 0.1 ha)	4.1 ± 1.5
Average snag dbh (cm)	16.1 ± 3.0
Percent coarse woody debris (%)	3.2 ± 1.8

Table 2.4 Home ranges estimates using MCP across the entirety of the northern flying squirrel range.

Home ranges (\pm SE) reported from 10 studies for adult northern flying squirrels using minimum convex polygon (MCP).

	Sex (n)	MCP (\pm SE) ha	Location
Urban 1988	M (3)	5.2 ± 1.1	West Virginia
Menzel et al. 2006	M (4)	59.8 ± 23.5	West Virginia
	F (8)	15.9 ± 8.7	
Diggins and Ford 2017	M (7)	5.8 ± 1.6	West Virginia
	F (6)	2.3 ± 0.5	
Weigl et al. 1999	M (6)	10.1 ± 3.3	North Carolina and Tennessee
	F (4)	6.9 ± 2.4	
Weigl et al. 2002	M (5)	20.3 ± 8.5	North Carolina and Tennessee
	F (2)	4.9 ± 0.1	
Diggins et al. 2017	M (10)	5.1 ± 1.2	North Carolina and Virginia
	F (10)	4.0 ± 0.7	
Witt 1992	Unknown (5)	$3.7 (0.5)$	Oregon
Wilson et al. 2008	M (9)	$28.6 (9.3)$	California
	F (4)	$23.8 (5.7)$	
Smith 2009	M (5)	9.0 ± 2.8	California
	F (17)	8.9 ± 1.6	
Hough and Dieter 2009	M (30)	11.2 ± 1.4	South Dakota
	F (19)	6.9 ± 0.9	
Holloway and Malcolm 2007	M (7)	11.2 ± 3.4	Ontario
	F (7)	3.8 ± 0.6	
Cotton and Parker 2000 ^a	M (9)	3.7	British Colombia
	F (6)	1.4	
Gerrow 1996 ^a	M (7)	12.5	New Brunswick
	F (8)	2.8	
This paper	M (6)	12.8 ± 6.1	West Virginia
	F (1)	4.8	

^a Only median values reported.

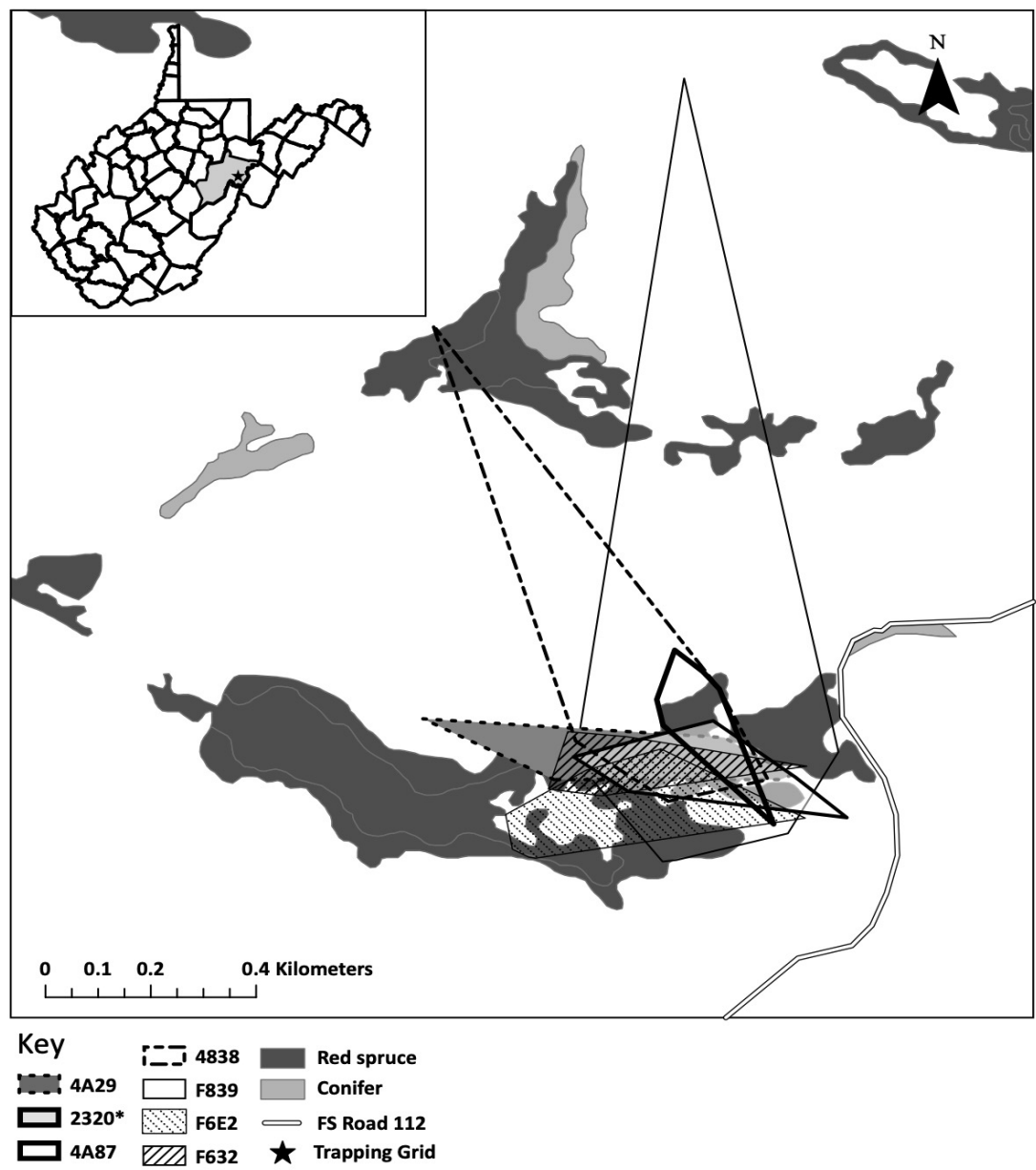


Figure 2.1 Map of home range estimates and overlap using MCP for 7 northern flying squirrels in a red spruce stand

Home range using minimum convex polygons for 7 adult northern flying squirrels, (*Glaucomys sabrinus fuscus*), 6 males and 1 female, denoted with an asterisk, in Randolph County, WV during the summer of 2019.

CHAPTER 3. HABITAT USE OF NORTHERN FLYING SQUIRRELS IN RELATION TO FINE-SCALE AND LANDSCAPE-SCALE CHARACTERISTICS IN A FRAGMENTED FOREST

3.1 Introduction

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) is a forest obligate species associated with high-elevation Allegheny forests dominated by mature red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), and mixed-conifer stands (Loeb et al. 2000; Mitchell 2001; Arbogast 2007; Smith et al. 2011) that include high densities of larger diameter trees, snags, and hypogeous fungi (Ford and Rodrigue 2007; Trapp et al. 2017). The Virginia northern flying squirrel's listing on the Endangered Species Act in 1985 resulted from surveys indicating low population numbers caused by habitat fragmentation and human disturbance (USFWS 2013). Following a review of their status, the USFWS delisted the squirrel in 2013 (USFWS 2013). Since their delisting, managers have focused on red spruce restoration projects to increase connectivity and extent of the squirrel's habitat within the MNF. Because this species occurs at low densities and in rugged and remote locations, efforts to minimize human costs while continuing to monitor the species' recovery and habitat use is of interest to land managers and researchers.

In West Virginia, red spruce experienced a range reduction of > 90% in the past century due to historical harvest practices for commercial timber products, slash burning post-harvest, and other anthropogenic factors (Allard and Leonard 1952; Stephenson and Clovis 1983). Red spruce forests are considered one of the most critically endangered ecosystems in the United States (Noss et al. 1995). Therefore, conservation and restoration of these red spruce forests have become a priority of the US Forest Service over the past 30 years. The 2006 Forest Inventory Plan (USFS 2006) identified nearly 60,000 ha within the Monongahela National Forest (MNF) available for

red spruce restoration. However, even without active restoration measures, red spruce has begun to gradually recover naturally. Researchers have recorded increases in red spruce within forest canopies (Fortney and Rentch 2003) and the understory at sites with stable or decreasing hardwood densities in hardwood-spruce ecotones (Rollins et al. 2010). Managing and increasing red spruce habitat is critical for supporting the viability of spruce-adapted wildlife species such as the Virginia northern flying squirrel.

Traditional survey methods for monitoring the northern flying squirrel population within the Monongahela have included live-capture methods or nest box monitoring (Ford et al. 2010). Both methods are labor intensive due to low capture rates, can induce stress in individual animals, and may result in trap or handling mortality. Mortality is especially concerning given their sensitive status post-delisting and low-density distribution across the landscape so there is a need for noninvasive monitoring protocols. Advancements in the use of automated detection for species-specific calls via ultrasonic acoustic monitoring have increased the use of this noninvasive survey method within the past 3 decades. Researchers have successfully implemented this survey method on a multi-national level for managing bats through the North American Bat Monitoring program (NABat), and the survey method has been used for other wildlife including birds (Hobson et al. 2002; Zwart et al. 2014; Cragg et al. 2016), anurans (De Solla et al. 2006; Gringas and Fitch 2013; Bedoya et al. 2014) and marine species (Josse et al. 1999; Barlow and Taylor 2005; Walters et al. 2011). This survey approach is especially useful for mammals that possess a high frequency or ultrasonic call repertoires which includes both species of North American flying squirrels (Britzke et al. 2013; Gilley 2013; Eisinger et al. 2016; Gilley et al. 2019).

Identifying northern flying squirrel calls can confirm presence at locations and when combined with occupancy modeling, can be used to evaluate detection or predict occupancy when

combined with habitat use. Researchers can apply automated methods for coarsely sorting call measurements, similar to those used when identifying bat calls, as an initial step to analyzing acoustic call data and then follow this with the more labor-intensive process of call identification and measurement. Unlike bats, where species-specific filters are available for sorting large quantities of data, current methods to categorize and confirm northern flying squirrel calls are based on visual descriptions and measurements of call characteristics including duration, frequency, and bandwidth among other measures (Eisinger et al. 2016; Gilley et al. 2019; Diggins et al. 2020).

I deployed acoustic monitors as a way to detect presence and estimate occupancy and habitat use of northern flying squirrels across red spruce gradients in the Monongahela National Forest. I deployed acoustic monitors in 31 forested stands within the 3 habitat quality categories, low, medium, and high described by Menzel et al. (2006) and based on vegetative community and elevation. I developed a coarse species-specific filter to automate the initial process of sorting through the large amounts of acoustic data recorded in the field and used measurements of call characteristics to confirm identity as northern flying squirrels. I then used these calls in combination with microhabitat measurements collected at the acoustic monitoring sites with occupancy modeling to describe the distribution of northern flying squirrels in relation to habitat and compared my results to those from a previous habitat model for this region (Menzel et al. 2006). I predicted that as characteristics associated with mature forests increase, such as percent red spruce, diameter at breast height (DBH), snag decay level, snag DBH, distance to the lowest branch, canopy cover, and percent coarse woody debris, the probability of occupancy of northern flying squirrels also would increase. I predicted that occupancy will be greatest in high quality habitat areas identified by the Menzel et al. (2006) habitat model.

3.2 Methods

3.2.1 Study Area

I deployed acoustic monitors within the Monongahela National Forest (MNF), West Virginia, USA in the USDA Forest Service (USFS) Cheat-Potomac, and Greenbrier Ranger Districts in forested stands classified as low-, medium-, and high-quality northern flying squirrel habitat (Menzel et al. 2006). Narrow valleys, broad ridges, and steep slopes of the Allegheny Mountains and Plateau sub-physiographic region of the Appalachian Mountains characterized the sites (Fenneman 1938; Byers et al. 2010). The climatic conditions of this region typically are cool and wet year-round with frequent fog. The annual average temperature is 6.7–9.4° C although freezing temperatures are possible throughout the year (Stephenson and Clovis 1983). The annual precipitation ranges from 120–150 cm with the majority from snow accumulation (Rentch and Fortney 1997). The elevation of the sites varied from 500 m to >1200 m. Red spruce was the dominant tree species in the highest elevation sites (>1200 m), with sparse understory cover primarily consisting of southern mountain cranberry (*Vaccinium erythrocarpum*), common bazzania liverwort (*Bazzania trilobata*) and flat fern moss (*Hypnum imponens*; Byers et al. 2010). Mid-elevations sites were mixed-hardwood forests with the greatest species diversity, where dominant tree species included red spruce, black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis* var. *alleghaniensis*; Byers et al. 2010). Other species less commonly found in the canopy included eastern hemlock, sweet birch (*Betula lenta*), striped maple (*Acer pensylvanicum*), and red oak (*Quercus rubra*). Tree saplings included red spruce, American beech (*Fagus grandifolia*), striped maple, and eastern hemlock; these species also dominated the understory, especially in stands with harvest activity in the last decade. Low elevation sites were extremely low in species

richness consisting almost entirely of red spruce and yellow birch with a dense understory of great rhododendron (*Rhododendron maximum*; Byers et al. 2010). All sites, with the exception of one, Fanny Bennett virgin forest, were second-growth stands and had experienced harvest in the last century. The USFS manages the areas surrounding my survey sites for multiple use, including recreation trails, timber harvest, roads, and wildlife openings.

3.2.2 Acoustic Monitoring

I deployed Song Meter SM4 and SM4BAT-FS acoustic monitors (Wildlife Acoustics, Maynard, Massachusetts) in 2 management areas on the MNF near Spruce Knob and Davis, West Virginia from 1 April–18 August 2019. The Song Meter SM4 has a recording range of 20–48 kHz, while the Song Meter SM4BAT-FS has a recording range of 16–500 kHz. Menzel et al. (2006) evaluated landscape-level characteristics and northern flying squirrel occupancy to develop a GIS-based habitat model. This model, which incorporated elevation and forest cover types, delineated low-quality, medium-quality, and high-quality habitat sites by likelihood of northern flying squirrel occupancy (Table 3.1). I used the GIS layers resulting from this model and provided by the USDA Forest Service to select acoustic monitoring sites in each of the habitat quality categories that occurred within the 2 management areas.

High-quality habitat sites included contiguous red spruce stands, conifer-dominated stands, and established nest box grids at higher elevations (> 1200 m). Medium-level habitat quality sites included a virgin conifer-dominated forest, mixed-hardwood conifer stands, and a site previously harvested using horses within the past decade all at moderate elevations (1000-1200 m). Low quality habitat sites include hardwood dominated stands and stands harvested within the past 10 years at low elevations (< 1000 m). I attached acoustic monitors to the bole of a tree 1.5 m above

the ground with an adjustable cable lock. I programmed the monitors to record from 2200–0600 hr for a minimum of 4 nights/site.

3.2.3 Habitat Surveys at Monitoring Sites

I quantified microhabitat conditions at each site according to the methods described in Bakker and Hasting (2002) by sampling a 0.1 ha plot around each acoustic monitor to include as covariates in the occupancy model. I measured the DBH and recorded species for every tree >10 cm DBH within the 0.1 ha area surrounding the acoustic monitor. I measured canopy cover with a concave spherical densiometer and height of the lowest living branch with a laser rangefinder. I also measured the DBH for snags and classified decomposition into 5 categories (Bush et al. 2009). I measured downed coarse woody debris (CWD) through log counts along each of the 16 m transects and averaged the 4 transects for the site. At each site, I classified the clutter into predetermined categories using visual inspection. I recorded the amount of clutter on a scale from 1-5 ranging from least to most cluttered, with 1 having a completely open understory whereas a category 5 site had a thick, dense understory comprised of shrubs, and tree saplings under 10 cm DBH. I recorded daily precipitation for each night an acoustic monitor was deployed using historical records of climatological observations from weather stations located in Bartow and Davis, WV from the National Oceanic and Atmospheric Administration (NOAA) through the National Centers for Environmental Information.

3.2.4 Analysis of Acoustic Data

I used Kaleidoscope Pro (v. 5.1.9i, Wildlife Acoustics, Maynard, Massachusetts) to filter non-target calls and identify potential northern flying squirrel vocalizations. Bats and northern flying squirrel calls can occur at similar frequencies; therefore, to eliminate bat calls from my

analysis, I used the Bat Auto ID function in Kaleidoscope Pro to identify and filter calls of the 15 native species of bat that potentially occur in the area. I filtered non-target sounds for each site by using a filter in non-bat analysis mode that only included sounds within the upper (300 kHz) and lower (6 kHz) vocalization frequency limits of the northern flying squirrel (Gilley 2013; Gilley et al. 2019). I initially classified the remaining acoustic outputs as either flying squirrel, bird, or white noise. White noise was ambient sound of neither vertebrate nor invertebrate origin and included precipitation, wind, or heavy machinery noise. When identifying calls as a northern flying squirrel, I also considered the time of the recording because flying squirrels are typically active from dusk to 2–3 hr after sunset and 1–2 hr before sunrise (Wells-Gosling and Heaney 1984). The majority of amphibian calls occurred immediately after sunset (2200 hr), and bird calls occurred prior to sunrise (0500 hr) during the dawn chorus (Brown and Handford 2003; Farina 2019). I initially classified all northern flying squirrel calls using previously published call parameters (Gilley 2013; Gilley et al. 2019; Diggins et al. 2020). I only measured characteristics from the first call in a call series using RavenPro (v. 1.6., Center for Conservation Bioacoustics 2019) using a frequency resolution of 512 DFT and Hann window with 50% overlap. Using the initial pulse in a series, I then measured call characteristics which included minimum frequency, maximum frequency, duration, Fmax, 90% bandwidth, average entropy. I also evaluated the general shape of the call as described by Gilley et al. (2019). I excluded any calls from additional analysis with a minimum frequency < 6.44 kHz, which was equivalent to 1 SD below the mean of the lowest call frequency described by Gilley (2013). I calculated dissimilarities among call characteristics and performed agglomerative nesting (AGNES) hierarchical clustering for the remaining calls using the R packages cluster, factoextra, and magrittr (v. 3.6.2 R Development Core Team 2017). Using the cluster analysis, I calculated the optimal number of clusters and a Hopkin's statistic for clustering

tendency using the R package NbClust (Charrad et al. 2014). I then excluded any calls that did not fit within the optimal cluster number and were grouped separately within the hierarchical cluster analysis.

3.2.5 Occupancy Modeling and Data Analysis

I used a single species, single season occupancy model with covariates using the RPresence package in program R (MacKenzie and Hines 2017). The detection history at each site represented a single season with each recording night serving as a replicate survey (e.g. 1010). I performed a Pearson's Product-Moment Correlation analysis on 9 initial habitat covariates to determine whether any covariates reflected duplication of a similar habitat variable (Puth et al. 2014). My final covariates included 7 occupancy predictor variables: percent of forest stand comprised of red spruce, percent canopy cover, average tree diameter at breast height (DBH), average height of the lowest living branch, percent coarse woody debris, average snag DBH, average snag decomposition class. Nightly precipitation, acoustic monitor type (either SM4 or SM4Bat-FS), and clutter were included as detection covariates. I developed a series of a priori models to evaluate the effects of habitat covariates and combinations of these covariates on the probability of occupancy of northern flying squirrels at different sites (Table 3.2). I used an information theoretic approach (Burnham and Anderson 2002; Arnold 2010) to evaluate potential models using habitat variables described in current literature to estimate northern flying squirrel occupancy (Bakker and Hastings 2002; Menzel et al. 2006; Smith 2007). After fitting the model, I calculated Akaike's Information Criterion (AIC_c), Akaike's weights (w_i), and the difference between the model with the lowest AIC_c and the AIC_c for the i th model (Δ_i). When examining the ranked models, I did not consider models for drawing conclusions if the parameters were a subset of parameters of the top model (Burnham and Anderson 2002).

3.3 Results

3.3.1 Acoustic Analysis

I obtained 376 survey nights total across 31 sites. The initial coarse filter in Kaleidoscope identified 133 potential northern flying squirrel calls. After measuring call characteristics in RavenPro and eliminating calls with a minimum frequency < 6.44 kHz, I used a total of 111 calls for the cluster analysis. Using measurements of call characteristics in the cluster analysis, I calculated a Hopkin's statistic = 0.87 suggesting that my data had a high level of clusterability (Adolfsson et al. 2019) with an optimal number of 3 clusters. I excluded 4 calls that fell outside the 3 main clusters, resulting in a total of 107 northern flying squirrel calls for use in the occupancy models. Based on the calls identified, I determined that of the 31 sites surveyed, I detected northern flying squirrels at 21 sites. I detected northern flying squirrels at 68% of all sites sampled, with northern flying squirrels detected at 15 sites on at least 2 nights. I detected northern flying squirrels at 7 of the 8 low habitat quality sites (Table 3.1). Within the medium quality habitat sites, I detected northern flying squirrels at 6 of 9 sampling sites. Lastly, within the high habitat quality sites, northern flying squirrels occupied 8 of 13 sites surveyed. I recorded 6 sites that had only 1 night with calls detected, and 15 sites ≥ 2 nights of calls detected.

3.3.2 Occupancy Modeling

I estimated overall occupancy (\pm SE) as 0.70 ± 0.01 for the low habitat quality sites, 0.75 ± 0.02 in the medium habitat quality sites and 0.81 ± 0.03 high habitat quality sites as defined by Menzel et al. (2006; Table 3.1). I estimated a probability of detection of 0.41 ± 0.05 across all 3 habitat use site categories. The model with a single detection covariate, clutter, was the highest ranked model at explaining the probability of detection of northern flying squirrels (Table 3.2).

The next highest ranking models included acoustic recorder type and precipitation. All the models including habitat covariates to explain the probability of occupancy ranked below the null models. Of the habitat covariates, the canopy cover was ranked highest but 9 of the 10 remaining models were within 2 Δi units. In general our single covariate models ranked higher than the models that incorporated multiple covariates (Table 3.1).

3.4 Discussion

3.4.1 Probability of Detection and Occupancy

My overall estimated probability of detection (\pm SE) using acoustic monitors was 0.41 ± 0.05 . Diggins et al. (2016) assessed the probability of detection for the endangered Carolina northern flying squirrel (*Glaucomys sabrinus coloratus*) and estimated the probability of detection \pm standard error for acoustic monitors was 0.37 ± 0.06 , compared to 0.01 ± 0.00 for live trapping. Capture success from live trapping northern flying squirrels has been reported as low as 1% in the Appalachian Mountains (Diggins et al. 2016) and as high as 78% on Prince of Wales Island, Alaska (Smith et al. 2004). Live-trapping can be limited when surveying remote locations and using nest boxes may bias the probability of detection in lesser-quality habitat where nesting locations are limited (Ford et al 2010). When live-trapping capture rates remain low within a study, capture-recapture data and minimum-number-known-alive data become unusable for predicting density (Ford et al. 2010). Ford et al. (2004) suggested that live-trapping efforts could potentially be reduced where northern flying squirrel occupancy could be reasonably assumed with confidence at sites with a predetermined level >0.75 probability of occupancy. Among the 3 habitat quality categories as described by Menzel et al. (2006), only my occupancy estimate for the low-quality habitat sites fell below that proposed threshold. I estimated occupancy within low quality sample

sites was 0.70, which was notably greater than the range (0–0.49) predicted by Menzel et al. (2006). Within medium habitat quality sites, I estimated occupancy was 0.75, which was at the upper end of the predicted range (0.50–0.75) for this habitat quality category (Menzel et al. 2006). For sites classified as high-quality habitat, I estimated likelihood of occupancy was 0.81, which was greater than the range (>0.75) predicted by Menzel et al. (2006). My estimates of occupancy fell within or were greater than the range predicted by Menzel et al. (2006) for all 3 habitat quality categories.

3.4.2 Detection Covariates

The top 3 highest ranked models, clutter, acoustic monitor model, and precipitation were all models with detection covariates. According to Adams et al. (2012) the detection of calls by an acoustic recorder is most affected by the frequency of the incoming signal, distance of the vocalization from the unit, and to a smaller degree, the detector angle. Vegetation structure such as clutter, canopy cover, and canopy height can also affect the efficiency of detection or obscure calls (O’Keefe et al. 2014). Patriquin et al. (2003) found that in open and thinned forests sounds with a frequency near 40 kHz were detected regardless of the complexity of the vegetation structure. However, sounds around 25 kHz were not as readily detected in these forested areas (Patriquin et al. 2003). Gilly et al. (2019) described several northern flying squirrel calls such as trills, tonal chirps, and arc chirps where the high frequency is approximately 25 kHz. These calls may be less likely to be detected in areas of high clutter. Additionally, areas with high levels of dense clutter may affect the quality of calls recorded with trails and forest openings more likely to produce identifiable calls than mature forests (Britzke 2003). Broders et al. (2004) concluded that the detection and classification of bat calls varied between sites with low, medium, and high levels of clutter in the overstory, which would be an important consideration as well for surveys for northern flying squirrels.

The type of acoustic monitor model, either Song Meter SM4 or SM4Bat-FS, was the second highest ranked model. There is significant variation in efficiency and efficacy among available automated acoustic detectors primarily due to differences in frequency sensitivity between models. For example, the microphone in each acoustic monitor model detects a subset of environmental sounds. However, the size and range of the subset of sounds recorded are heavily determined by the model. Therefore, depending on the model of acoustic monitor used, different detectors will yield different results and must be considered based on the vocal range of the focal species (Adams et al. 2012). For monitoring northern flying squirrels, I recommend an acoustic monitor model similar to the Wildlife Acoustic's SM4Bat-FS. This model reduced the amount of white noise and non-target species recorded and the calls were easier to identify based on their similarities to calls described in the literature.

Precipitation was the third highest ranked detection model. Weigl (1974) concluded that while inclement weather such as high wind speeds, thick mist, or heavy precipitation did not inhibit northern flying squirrel movement entirely, the timing of nightly movement was greatly delayed, and individuals tended to remain near the nest site. Gliding, the primary method of locomotion, is restricted in heavy rainfall due to poor visibility and difficulty climbing to appropriate launch points. Weigl (1974) noted that during periods of inclement weather, individuals moved among trees using branches rather than gliding thereby reducing the total distance traveled throughout the night. As precipitation increased, the likelihood of detection decreased. This is likely due to the short detection range of the acoustic monitors and the alteration in behavior, which can diminish the nightly distance traveled.

3.4.3 Occupancy Covariates

Past habitat models for northern flying squirrels in the Appalachian region used coarse-grained landscape features to identify areas of high conservation priority (Odom et al. 2001; Menzel et al. 2004; Menzel et al. 2006). However, Ford et al. (2004) suggested that to reduce uncertainty, future efforts should focus on defining macro- and micro-habitat associations for the Virginia northern flying squirrel in the high-elevation forests of the central Appalachians. The model that incorporated habitat quality categories and the models with habitat covariates measured at the acoustic monitoring sites did not perform better than the null model. This suggests that the methods used to measure the habitat covariates or the habitat covariates I measured did not effectively predict northern flying squirrel occupancy in the forest stands monitored with acoustics. The fifth highest ranking model used the habitat categories described by Menzel et al. (2006) to predict northern flying squirrel occupancy. The habitat categories within the Menzel et al. (2006) model incorporated elevation and habitat type as variables, and this model ranked higher than other covariates measures. This suggests that the combination of landscape level covariates such as elevation, and microhabitat characteristics are better predictors of northern flying squirrel occupancy. While Menzel et al. (2006) did not use acoustics monitors to assess occupancy for their modeling, this likely does not account for the occupancy estimate discrepancies between the habitat quality categories in this study.

Greater canopy cover is an indication of habitat structure that supports gliding and may be directly related to habitat type included in the habitat quality categories as described by Menzel et al. (2006). Flying squirrels traveling in unforested, open areas where there might be large gaps within the canopy likely expend more energy than when dispersing through closed canopy forested habitats (Adler and Kotar 1999; Flaherty et al. 2010). Furthermore, open canopy areas may be more energetically expensive as these areas lack insulation for cold weather, and individuals are

directly exposed to precipitation (Flaherty et al. 2010). Forests with closed, high canopies provide higher launch points with unobstructed gliding, allowing for longer, more energy-efficient movement (Dial 2003; Flaherty et al. 2010). Greater canopy cover also may provide protection against predators in the upper canopy (Pyare and Longland 2002). Specifically, canopy cover reduces the amount of understory lunar illumination which reduces the predation risk from some species of owls (Kotler et al. 1991; Longland and Price 1991).

Snag decomposition class and snag DBH, as single habitat covariate models were the seventh- and eighth-ranked models respectively at explaining northern flying squirrel occupancy within my sample sites. Holloway and Malcolm (2006) found a strong relationship between the density of large spruce, snags, and northern flying squirrel densities in Ontario. Large diameter trees provide a larger gliding landing and launch structure (Vernes 2001). Researchers also have documented northern flying squirrels nesting in large diameter trees and snags (Carey et al. 1997; Cotton and Parker 2000; Baaker and Hastings 2002; Pyare et al. 2010). Depending on availability, flying squirrels nest in either live trees with cavities or in snags (Cotton and Parker 2000). In my, study we did not observe flying squirrels nesting in snags. However, northern flying squirrels preferentially select snags because they offer more cavities than do live trees, especially in managed forests where large trees are rare (Carey et al 1997; Meyer et al. 2005). Snag decomposition class is also highly important as flying squirrels are secondary cavity nesters (Newton 1994; Martin et al. 2004). Because primary nesters, such as woodpeckers, tend to prefer snags with high levels of wood boring insects and soft, decayed wood that allows for excavation (Martin et al. 2004), snags with higher levels of decomposition are more likely to contain cavities that northern flying squirrels use for denning. Smith et al. (2005) noted that the northern flying squirrel's response to specific habitat features rely greatly on the relative abundance in a given

landscape where features in low abundance are limiting factors. Therefore, within my sampling sites, the relationship between snags and northern flying squirrel occupancy can be potentially explained with snags as a limiting habitat factor influencing microhabitat use.

The association between high elevation conifer forests with a spruce component and northern flying squirrel occurrence has been well documented likely because of the association of this conifer tree with mycorrhizal fungi (Payne et al. 1989; Odom et al. 2001; Ford et al. 2004). In the central Appalachians, fungi and lichen comprise a large portion of the northern flying squirrel diet (Mitchell 2001). Loeb et al. (2000) found that hypogeous fungi vary in abundance and distribution, and the presence of truffles was directly linked to the presence of red spruce rather than northern hardwood species. Similarly, researchers and managers use the presence of conifer species as a proxy for an abundance of food resources for the northern flying squirrel at the microhabitat scale in the Pacific Northwest (Pyare and Longland 2002). However, red spruce ranked 9 out of the 15 a priori models, therefore habitat-type alone may not be sufficient to accurately predict northern flying squirrel occupancy, especially when considering diet composition. Trapp et al. (2017) concluded that the diet of the Virginia northern flying squirrel consisted primarily of hypogeous fungi, epigeous fungi, and invertebrates contributing to >65% of the overall diet as a group. However, due to similarities in isotopic signatures, Trapp et al. (2017) was unable to conclude which of the 3, hypogeous fungi, epigeous fungi, or invertebrates, contributed the most to the overall diet. Epigeous fungi were the most readily available in the conifer dominated habitat, and arboreal lichen is available across both conifer and hardwood habitats, suggesting that hypogeous fungi may not be a limiting factor in the northern flying squirrel diet (Selva 1994; Trapp et al. 2017).

Comparatively, covariates that did not rank as highly included lowest living branch height and percent coarse woody debris. Coarse woody debris in second-growth forested stands of the Appalachian Mountains is generally associated with hypogeous fungi, a core component of the northern flying squirrel diet (Hackett and Pagels 2003). However, my sample sites had low volumes of coarse woody debris. Pyare and Longland (2002) did not find a relationship between coarse woody debris, an important habitat feature for fungal growth, and northern flying squirrel occurrence. Pyare and Longland (2002) suggested that simple counts of logs may not reflect the abundance or diversity necessary to support conditions for fungal growth. Additionally, my study site had a relatively homogenous litter layer relative to the mixed-conifer sampling sites (Meyer et al. 2007). Therefore, coarse woody debris may not have represented a strong proxy for hypogeous fungi and a predictor of northern flying squirrel occupancy (Tradeau et al. 2011).

Lowest living branch provides an indication of mid-story canopy structure. A relatively open mid-story allows for a higher gliding launch point and unobstructed gliding space (Scheibe et al. 2006). Excessive mid-story clutter does not facilitate unobstructed gliding locomotion, which prevents energy savings from long distance gliding (Vernes 2001; Scheibe et al. 2006; Flaherty et al. 2010). The height of the lowest living branch may be a measure of clutter and therefore a better predictor of detection than occupancy. Because the height of the lowest living branch was relatively homogenous across all sample sites, it likely was not a strong proxy for mid-story development or complexity.

Trapp et al. (2017) concluded that managers should give greater consideration to stand age and complexity than focusing on habitat type when managing for northern flying squirrels. Smith (2007) suggested that further research should be conducted to determine whether young growth forests can sustain long term populations of northern flying squirrels, but concluded that the

dependence on old-growth structural features is determined by the northern flying squirrel autecological requirements and the local ecological community. However, young growth stands do not provide the dense canopies, open midstory, and large tall trees necessary for efficiently gliding, accessing patchily distributed food resources and denning (Smith 2007; Manning et al. 2012). Therefore, older stands are more likely to provide the necessary habitat features required by this species regardless of dominant tree species.

3.4.4 Suggestions for Future Acoustic Survey Efforts

Acoustic monitoring, while challenging, presents a promising method to non-invasively monitor the northern flying squirrel. When conducting acoustic surveys quantitative measures of vegetation structure such as live tree basal area, canopy crown volume and midstory stem count should be used to quantify clutter (O’Keefe et al. 2014). Furthermore, precipitation and heavy winds affect the probability of detection. I recommend conducting acoustic surveys during periods of low inclement weather and excluding survey nights with heavy precipitation or wind. The amount of data generated can be addressed by first limiting non-target sounds prior to monitor deployment through acoustic monitor model selection and then by filtering recorded sounds after deployment. Recording settings also limit the collection of non-target sounds. Currently, software such as Kaleidoscope uses pattern recognition to filter sounds into similar clusters but lacks the capability to differentiate vocalizations from background clutter. Unfortunately, current methods for call detection show high sensitivity to noise or background clutter, and poor recall rate (Priyadarshani et al. 2017). Existing call libraries used to identify and train models for software were recorded in a lab setting (Gilley 2013; Gilley et al. 2019) and the difference in quality between lab and field calls may result in some challenges with analysis. For example, calls recorded in the field may lack volume and clarity because of the calling individual’s distance from the recorder

and other biological sounds that create background clutter. I recommend measuring call characteristics and running a cluster analysis to reduce subjectivity in call identification. Additionally, when examining output clusters for northern flying squirrels, I recommend considering the time at which the call was recorded to aid in the overall identification certainty. Recent advancements in pattern recognition include successfully identifying rain in field recordings (Bedoya et al. 2017) and identifying the dominant sound source within an individual recording (Bellisario et al. 2019). I also recommend using acoustic monitors similar to the SM4Bat-FS model (recording range of 16–500 kHz) for northern flying squirrels. Captured calls using this model were more similar in frequency to those reported in the literature, easier to identify, and this model reduced acoustic bycatch. The SM4 (range 20–48kHz) captured a greater amount of white noise, especially at the low end of the call range. Traditional acoustic monitor settings include 59-min recording windows which result in large .wav files. This data length and size can be difficult to analyze. Belisario et al. (2019) used a recording duration of 10 minutes, with a sampling frequency of 44,100 Hz with 16-bit and 23 ms viewing frame. These parameters provided for additional analysis which aids in the automation of call identification without loss of data necessary for occupancy modeling (Belisario et al. 2019). New tools that aid in the speed and accuracy of classification for biological sounds (Zhang et al. 2016) and analyses will continue to improve methods for acoustic sampling of free ranging wildlife leading to greater adoption of this non-invasive method.

3.5 Management Implications

In my study, the habitat characteristics measured did not efficiently predict the probability of occupancy for northern flying squirrels. Future efforts to model northern flying squirrel occupancy should measure additional microhabitat features and characteristics that initially focus

on stand age. Habitat characteristics related to stand age should be a main priority for managers focused on improving northern flying squirrel habitat in the southeastern US. Management activities and silvicultural practices that reduce characteristics of structural complexity, including canopy cover and large diameter trees, can result in lower population density (Smith 2007). Altering forest structure and complexity affects food and den site availability as well as predation rates (Smith 2007). I suggest for each proposed silvicultural treatment incorporating location of treatment, size, and number with spatially-explicit modelling to examine the potential long term effects on dispersal, home range establishment, metapopulation connectivity, and population demographics before implementing management activities (Trapp et al. 2019). Additional research using acoustic monitors with the northern flying squirrel will further refine methods and analysis. I recommend acoustic monitoring as a non-invasive survey method to document species occupancy that can be applied at large landscape scales where traditional methods are not logistically feasible, especially for rare, cryptic species such as the Virginia northern flying squirrel.

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Table 3.1 Acoustic monitor sites surveyed, number of call detections and occupancy estimates for 3 habitat quality categories.

Number of sites surveyed, site occupancy, number of call detection nights and estimated occupancy for northern flying squirrel habitat quality categories as described by Menzel et al. (2006) in the Monongahela National Forest, WV in 2019. High quality habitat sites included contiguous red spruce stands, conifer dominated stands, and established nest box grids. Medium-level habitat quality sites included a virgin forested area, mixed-hardwood conifer stands, and a site previously harvested using horses within the past decade. Low quality habitat sites included hardwood dominated stands and young-growth stands harvested within the past 10 years.

	Sites surveyed	Sites detected	> 1-night call detection	\geq 2-nights call detection
Low	8	7	1	6
Medium	9	6	4	2
High	13	8	1	7

Table 3.2 Parameters and rankings for occupancy model outputs.

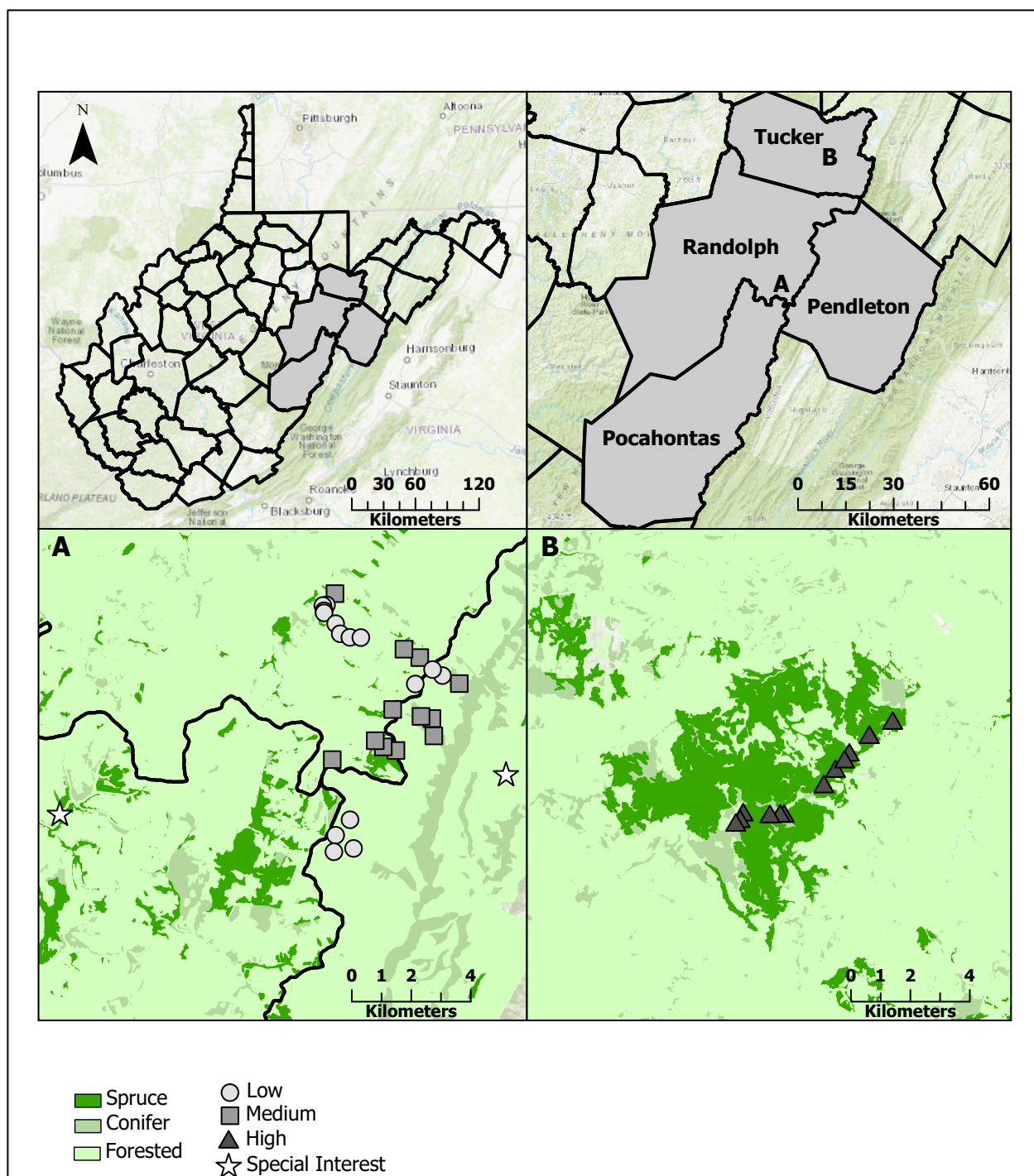
Number of estimated parameters (K), Akaike's Information Criteria (AIC_c), difference between model AIC and the best model (Δi), and Akaike's Weight (W_i) used to model northern flying squirrel occupancy in the Monongahela National Forest, WV in 2019.

Model	K	AIC_c	Δi	W_i
psi() p(Clutter)	3	187.7472	0.0000	0.5476
psi() p(Recorder)	3	190.7181	2.9639	0.1244
psi() p(Precipitation)	3	191.6008	3.8466	0.0800
psi() p()	3	193.2238	5.4696	0.0355
psi(Habitat quality) p()	3	193.3743	5.6201	0.0330
psi(Canopy cover) p()	3	193.6369	5.8827	0.0289
psi(Snag DBH) p()	3	193.8890	6.1348	0.0255
psi(Snag class) p()	3	193.9952	6.2410	0.0242
psi(Red spruce) p()	3	194.1388	6.3846	0.0225
psi(Snag class + canopy cover) p()	4	194.7768	7.0226	0.0163
psi(Tree DBH) p()	3	194.8404	7.0862	0.0158
psi(Tree DBH + snag DBH) p()	4	194.9073	7.1531	0.0153
psi(Branch height) p()	3	195.1928	7.4386	0.0133
psi(CWD) p()	3	195.2103	7.4561	0.0132
psi(RS + BH + snag DBH) p()	5	197.3579	9.6037	0.0045

Table 3.3 Model parameter estimates, standard error (SE) and 85% confidence intervals (CI).

Model parameter estimates, standard error (SE) and 85% confidence intervals (CI) for the top 4 models used to predict northern flying squirrel occupancy in the Monongahela National Forest from April-August 2019.

Model	Estimate \pm SE	Upper 85% CI	Lower 85% CI	P-value
Clutter	0.46 \pm 0.44	1.09	-0.18	<0.001
Recorder type	0.91 \pm 0.40	1.48	0.33	0.02
Precipitation	-0.88 \pm 0.62	0.01	-1.77	0.16
Intercept only	1.05 \pm 0.19	1.32	0.78	0.03



CHAPTER 4. SUMMARY

4.1 Summary

Collectively, my thesis provides information on northern flying squirrel habitat use in relation to fine-scale and landscape-scale characteristics in a fragmented forest. My thesis documents northern flying squirrel home range size, home range overlap, den site preferences, and microhabitat use within a red spruce stand before restoration activities. These data serve as baseline information for existing habitat conditions and current habitat use. Post-implementation of the silvicultural treatments, these data will aide managers in monitoring changes in habitat use by northern flying squirrels.

Researchers have previously reported negative effects on squirrel densities after the application of thinning and similar silviculture techniques (Holloway and Smith 2011; Manning et al. 2012). I measured microhabitat characteristics that are significantly impacted during canopy-gap thinning silviculture treatments including the density of conifers, lowest living branch height, coarse woody debris, and snag density in a site before restoration (McGee et al. 1999; Holloway and Malcolm 2006). I found that a majority of northern flying squirrel locations were directly within the red spruce stand and that flying squirrels were preferentially selecting large diameter trees for nesting locations. As a result of the close association of the northern flying squirrel within these remnant red spruce stands, I recommended caution using small-scale silvicultural treatments. There is evidence of gradual red spruce recovery and thinning significantly impacts microhabitat characteristics associated with squirrel occupancy. Given flying squirrels already exist at low densities on the landscape, further habitat disturbance may lead to a future decrease in population density on harvested sites (Holloway and Malcolm 2006; 2007).

Previous efforts to model northern flying squirrel occupancy and identify areas of high conservation priority relied on stand and landscape-level features (Odom et al. 2001, Menzel et al. 2006). My research aimed to identify fine-scale microhabitat characteristic associations that predict northern flying squirrel occupancy across a gradient of red spruce stands and levels of habitat quality. In this study, canopy cover was the single greatest predictor of squirrel occupancy. However, all covariates in the highly ranked occupancy models were a proxy for stand age and complexity. I concluded that when evaluating northern flying squirrel habitat managers should not exclusively consider habitat type in isolation but should focus management on characteristics of stand age and complexity.

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