

**RESOURCE SELECTION, HOME RANGE AND HABITAT ASSOCIATIONS OF
THE SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) IN THE
PIEDMONT AND COASTAL PLAIN OF VIRGINIA**

Marissa Hahn Guill

Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

IN

FISHERIES AND WILDLIFE SCIENCES

W. Mark Ford, Committee Chair

Verl Emrick

Mike Cherry

July 27, 2023

Blacksburg, Virginia

Keywords: Coastal Plain, habitat, home range, occupancy, prescribed burn, resource selection,
Southern fox squirrel, *Sciurus niger niger*, Virginia

RESOURCE SELECTION, HOME RANGE AND HABITAT ASSOCIATIONS OF THE SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) IN THE PIEDMONT AND COASTAL PLAIN OF VIRGINIA

Marissa H. Guill

ACADEMIC ABSTRACT

The southern fox squirrel (*Sciurus niger niger*) has the northernmost part of its range in Virginia. For the past 100 years, southern fox squirrels have been declining due to habitat fragmentation, cover type conversion, and fire suppression. Decrease in growing season burns, hardwood encroachment and forest mesophication have transformed pine hardwood woodlands and pine (*Pinus* spp.) savanna habitats that southern fox squirrels prefer to hardwood dominant habitats that eastern gray squirrels (*Sciurus carolinensis*) prefer. These habitat changes have the potential to increase competition among the two species.

The main objectives of my study were to investigate the general resource needs, occupancy, and home range of southern fox squirrels as well as the impact of resource partitioning and possible competition with eastern gray squirrels in the Piedmont and Coastal Plain of Virginia. I captured, radio collared and tracked four individuals at Big Woods Wildlife Management area and Piney Grove Complex using 95% and 50% kernel density estimate. I found an average male home range 176.49 ha (SE = 25.73, $N = 2$) and 40.62 ha (SE = 5.87, $N = 2$) and an average female home range of 28.51 ha (SE = 0.49, $N = 2$) and 4.71 ha (SE = 0.34, $N = 2$). I then identified the second and third order habitat selection in which my top models identified selection for pine savanna cover types ($\beta = 2.095$, SE = 0.158), increasing number of burns since 2019 ($\beta = 1.24$, SE = 0.098), and decreased time between burns ($\beta = -0.233$, SE = 0.097).

I used two-species occupancy modeling which reflected that gray squirrel occupancy increased with increasing time since last prescribed burn. However, southern fox squirrel occupancy, in the absence of gray squirrels, decreased with increasing time since last burn. My informed single-season occupancy model confirmed that southern fox squirrel occupancy decreased with time since the last burn. Presence in the absence of gray squirrels suggests that southern fox squirrels are selecting habitats on BWPGC with respect to both resource needs and competition with gray squirrel. Additionally, my level-of-effort (LOE) analysis indicated that 7 consecutive days of camera trapping without a southern fox squirrel detection would provide 90% confidence of the species' absence in areas burned 2 or more years prior to sampling in southeastern Virginia. Further management for southern fox squirrels in the future should focus on high rotational (short fire return interval) burns in areas of savanna as well as pine-hardwood mixed areas and hardwood-pine savanna ecotones.

**RESOURCE SELECTION, HOME RANGE AND HABITAT ASSOCIATIONS OF
THE SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) IN THE
PIEDMONT AND COASTAL PLAIN OF VIRGINIA**

Marissa H. Guill

GENERAL AUDIENCE ABSTRACT

The southern fox squirrel (*Sciurus niger niger*) is a subspecies of fox squirrel that ranges from southeastern Virginia down to northern Florida. All throughout its range in the Southeast, southern fox squirrel habitat has been fragmented from natural mixed pine-hardwood woodland forests to agriculture and high rotation pine plantations. Additionally, habitat has been further transformed by the lack of prescribed fire as a management tool on the landscape. This has in turn created sparse and fragmented local populations of southern fox squirrels as well as possible competition with gray squirrels. Further, the southern fox squirrel has not been studied in Virginia in over 20 years and management recommendations are lacking.

I studied the resource needs, occupancy, home range and competition of southern fox squirrels in two physiographic regions of Virginia: the Coastal Plain and Piedmont regions. The Coastal Plain field site was Big Woods Wildlife Management Area and The Nature Conservancy's Piney Grove- both adjacent to each other. The Piedmont field site was Military Training Center Fort Barfoot. Here I utilized camera trapping, nest box monitoring, live trapping, and radio tracking to assess the resources they are utilizing in each area through home range analyses. I found that southern fox squirrels are selecting areas that have low fire return intervals and are located in pine savanna habitats. Therefore, fire should be prioritized as a management tool for southern fox squirrel habitat in pine savanna areas. I also used camera trapping data to identify the possible competition among gray and fox squirrels and fox squirrel detection through occupancy modeling. My findings reflected that there is apparent competition between southern fox squirrels and eastern gray squirrels and that southern fox squirrels are selecting heavily burned areas not only for their resource needs, but also because gray squirrels are absent.

I concluded through my studies that the southern fox squirrel currently occupies southeastern Virginia, particularly in the Coastal Plain, however at low numbers. This could be due to suitable habitat on Big Woods/Piney Grove, but the surrounding habitat is of marginal quality. Further, in documenting southern fox squirrels, multi day camera surveys in mixed pine-hardwood woodland and pine savannas should be prioritized. Also, in aims to increase the presence of southern fox squirrels on the landscape, short rotation prescribed burning should be prioritized as well as additionally considering competition among gray squirrel and fox squirrel competition.

ACKNOWLEDGEMENTS

Funding to Virginia Polytechnic Institute and State University for this project was provided by the Virginia Department of Wildlife Resources from the US Fish and Wildlife Services' Wildlife and Sportfish Restoration Program (award F18AF00664) provided by the US Fish and Wildlife Service's Wildlife and Sportfish Restoration Program and Virginia Department of Military Affairs contract 2018-040 made this project possible. I want to further thank the Nature Conservancy for allowing access to the Piney Grove Preserve to conduct this research. More specifically, I want to thank Bobby Clontz, Brandon Martin, Matthew Kline, Ken Oristaglio, David Phillips, Matthew Fields, Marcelo Jorge, and Caroline Bryant for all of their hard work in logistical support and field assistance. None of this would have been possible without them! I also want to specifically thank Marc Puckett, your enthusiasm for this project and efforts in helping with all moving parts from equipment to funding were incredibly helpful and immensely appreciated.

Thanks to the entire Ford lab for their help in all things involving graduate school. Although lives were busy, I have enjoyed meeting every single one of you and your presence and encouraging words alone helped me through some of the most stressful days. None of my analysis would have been possible without the support and patience of Jesse De La Cruz. I truly appreciate all your help in answering hundreds of emails, forcing me to appreciate and use R Studio, and mentoring me in all facets to make me a successful graduate student and person. I could not have done it without your guidance.

I am further grateful for everyone at the Conservation Management Institute at Virginia Tech, especially Dr. Verl Emrick, Mike St. Germain, and Scott Klopfer as I would not be here today without them. Thank you for giving me some of my first opportunities, for pushing me to become a naturalist and for preparing me to be a successful graduate student. I would also like to thank my committee for guidance, including Dr. Mike Cherry for supporting this project from states away. I would like to thank my advisor, Dr. Mark Ford, for giving me this opportunity and pushing me to new limits that I never thought I could reach. Your guidance, and support for myself and this project throughout many years of learning curves and navigating gnarly COVID times is something I am incredibly grateful for. I really could not have done it without your mentorship. Thank you for believing in me, sharing a fascination for squirrels, and most importantly introducing me to the Virginia Diner. I will forever boast about how I was a graduate student under THE Mark Ford.

Lastly, thank you to all of my family and friends who have supported me these past few years. To my husband Tyler, thank you for all of your love, encouragement, and patience. Thank you for being there for me during the downs and celebrating with me during the highs. Life only gets better from here. To my sister, Emily Hahn, thank you for being the first one I always call with my frustrations and triumphs and for being the best sister someone could ask for. To my mom and dad, Marianne and Steve Hahn, thank you for being there for me always and teaching me that hard work pays off. I would not be the person I am today without any of you.

TABLE OF CONTENTS

Academic Abstract.....	ii
General Audience Abstract.....	iii
Acknowledgements.....	iv
Table of Contents.....	v
Chapter I: Introduction.....	1
History of fox squirrels in the U.S.....	1
Study Site.....	4
Literature Cited.....	8
Figures.....	11
Chapter 2. Resource selection of the Southern Fox Squirrel (<i>Sciurus niger niger</i>) in the Piedmont and Coastal Plain of Virginia.....	13
Introduction.....	13
Methods.....	15
Live Capture.....	15
Tracking and Telemetry.....	17
Statistical Analysis.....	18
Results.....	20
Discussion.....	21
Literature Cited.....	25
Tables and Figures.....	30
Chapter III. Southern Fox Squirrel (<i>Sciurus niger niger</i>) and Eastern Gray Squirrel (<i>Sciurus carolinensis</i>) interactions in a rare, fire-maintained ecosystem.....	39
Introduction.....	39
Methods.....	41
Camera Surveys.....	41
Predictor Variables.....	43
Data Analysis.....	44
Two-Species Occupancy Modeling.....	45
Single-Species Modeling and Level of Effort (LOE) Estimation.....	46
Results.....	47

Discussion.....	48
Literature Cited.....	52
Tables and Figures.....	58
Chapter IV. Conclusions and Management Implications.....	66
Virginia Piedmont and Coastal Plain Associations.....	66
Future Habitat Management.....	66
Appendix A, B, C, and D: Supplemental Tables, Figures, and Pictures.....	58
Appendix A. Den site characteristics for southern fox squirrels (<i>Sciurus niger niger</i>) at Big Woods Wildlife Management Area and Piney Grove Preservation, Virginia, October 2022.....	69
Appendix B. Species distribution models of southern fox squirrels (<i>Sciurus ., niger</i>) in the Coastal Plain Regions of Virginia, 2020-2022.....	73
Species distribution models of the southern fox squirrel in the Coastal Plain of Virginia.....	74
Tables and Figures.....	76
Literature Cited.....	83
Appendix C. Example of identified southern fox squirrels (<i>Sciurus niger niger</i>) from remote trail camera locations at Big Woods WMA, Piney Grove Preservation and Fort Barfoot, Virginia, October 2019- October 2020.....	85
Appendix D. Examples of identified southern fox squirrels (<i>Sciurus niger niger</i>), gray squirrels (<i>Sciurus carolinensis</i>), southern flying squirrels (<i>Glaucomys volans</i>) and other inhabitants from nest box locations at Big Woods WMA, Piney Grove Preservation, and Fort Barfoot, November 2020-June 2022.....	94

CHAPTER I: GENERAL INTRODUCTION AND BACKGROUND

History of Fox Squirrels in the Southeastern U.S.

Historically, the range of the fox squirrel species (*Sciurus niger*) spanned the eastern United States from Canada to Mexico. Fox squirrels currently occupy much of this range (Trani et al. 2007), with stable to abundant populations in the Midwest and central Appalachian Mountains (Edwards and Laerm 2007). However, fox squirrel populations east of the Appalachians have steadily declined over the last 100 years due to changes in habitat quality and extent (Edwards and Laerm 2007). In Virginia, there are two subspecies of fox squirrel listed as at risk per the State Wildlife Action Plan (VDWR 2015); the Delmarva Peninsula fox squirrel (*S. n. cinereus*), a recently delisted federal endangered species (USFWS 2015) and southern fox squirrel (*S. n. niger*). The southern fox squirrel holds a status at tier III (high conservation need) and a conservation opportunity rating of A (identifiable habitat management strategies expected to benefit the species) (VDWR 2020).

Specifically, the southern fox squirrel, one of ten subspecies of the fox squirrel, ranges from northern Florida to southeastern Virginia (Figure 1; Edwards et al. 2003). Much of the southern fox squirrel's habitat in the Piedmont and Coastal Plain physiographic regions has declined in quality and extent from conversion and fragmentation of pine (*Pinus* spp.) savanna and mixed pine-hardwood forests areas to agriculture, working pine plantations, and development (Edwards et al. 2003). Further, natural pine forests in the Southeast decreased from over 28 million ha to less than over 10 million ha since 1952 (Wear and Gris 2002).

In addition, the Piedmont and Southeastern Coastal Plain regions of the U.S. have higher degrees of ‘natural condition’ habitat loss than any other ecoregion in the eastern U.S. (Martinuzzi et al. 2015). In the Southeast, forests maintained by frequent fire with reduced understory and midstory woody vegetation have more abundant populations of southern fox squirrels (Boone et al. 2017). Higher cover of grasses and forbs in the understory allow the southern fox squirrels to move rapidly through the habitat (Edwards et al. 1998, Greene and McCleery 2017).

Land conversion has decreased the availability of important microsite habitat components for southern fox squirrels such as natural cavities for denning, and favored hard- and soft-mast food sources. Specifically, conversion to short rotation pine plantations eliminates oak mast, and to some degree pine mast, and rarely provides cavity den opportunities (Whitaker and Hamilton 1998). Denning structures, such as drey (leaf) nests and tree cavities, are an important habitat component for all subspecies of fox squirrels for protection from predators, inclement weather, and rearing young. Thus, they require, in part, mature forests or some mature forest attributes for denning habitat, along with hard mast producing species (Koprowski 2005). In Virginia, southern fox squirrels may preferentially select hardwood bottomland edges adjacent to short-rotation pine plantation cover to maximize access to mast and suitable denning trees (Loeb and Lennartz 1989). However, data on status, range, and habitat associations for the southern fox squirrels in Virginia are lacking.

Information about southern fox squirrel habitat associations in the Coastal Plain and particularly the Piedmont regions of the United States is limited or very site-specific in nature. However, Edwards et al. (1989) in the Coastal Plain of South Carolina, and

Prince et al. (2014), Prince et al. (2016), and Steele et al. (1992) in the Coastal Plain of North Carolina, similarly observed the importance of pine dominated forests (shortleaf pine, *Pinus echinata* and longleaf pine, *Pinus palustris*.) and home ranges localized to foraging habitats. Edwards et al. (1998) noted southern fox squirrels using mature loblolly pine (*Pinus taeda*) savannas in the Piedmont of Georgia. Although these studies examined intact habitat and appropriate landscapes, they do provide baseline information that can inform aspects of the ecology of southern fox squirrels in the Virginia Piedmont and Coastal Plain. At present, there have been no empirical assessments on distribution, population status or home range/habitat use for southern fox squirrels in southeastern and south-central Virginia.

Project Background and Goals

The Conservation Management Institute, the Virginia Tech Department of Fish and Wildlife Conservation, and the U.S. Geological Survey Virginia Cooperative Fish and Wildlife Research Unit at Virginia Tech cooperated with the VDWR to examine the distribution, abundance, and habitat use of southern fox squirrels in the landscape surrounding study sites in the Piedmont and Coastal Plain regions of Virginia. Initial efforts were directed at the completion of squirrel nest boxes deployed at both Fort Barfoot (Formerly Military Training Center Fort Pickett) and at the Big Woods Wildlife Management Area and Piney Grove Reserve. The purpose of the nest boxes was to enhance availability of nesting/roosting activities for southern fox squirrels and to attract any local individuals to facilitate monitoring and potential capture. For my research, I had three primary objectives: (1) to assess the general resource needs that southern fox squirrels are utilizing in the Piedmont and Coastal Plain regions of Virginia, (2) to assess

the general occupancy and home range status of southern fox squirrels in these regions, and (3) to investigate the impact of resource partitioning and possible competition among southern fox squirrels and gray squirrels (*Sciurus carolinensis*).

STUDY SITE

Data collection took place at Fort Barfoot and the Nature Conservancy's Piney Grove Preservation and Big Woods Wildlife Management Area (Figure 2). The Fort Barfoot is located in the predominantly rural piedmont physiograph of southeastern Virginia, approximately 5 km east of the town of Blackstone and approximately 25 km west of the fall line demarcating the coastal plain (Figure 2). Fort Barfoot encompasses 16,592 ha of land in three counties: Nottoway (8647 ha), Brunswick (2645 ha), and Dinwiddie (5300 ha). This province of southeastern Virginia, approximately 5 km east of the town of Blackstone and approximately 25 km west of the fall line demarcating the coastal plain (fig. 2). Fort Barfoot encompasses 16,592 ha of land in three counties: Nottoway (8647 ha), Brunswick (2645 ha), and Dinwiddie (5300 ha). It consists of mixtures of deciduous, pine, mixed pine-hardwood, and bottomland hardwood forests with open shrub and grasslands throughout. Additionally, Fort Barfoot has had a history of fire-maintained disturbance from both military training and stewardship, maintaining habitat conditions and structure that may have more approximated natural conditions regionally (Kalen et al. 2014, Emrick et al. 2018).

Fire return intervals average 2-4 years at Fort Barfoot. It also contains a 4,521 ha buffer for the impact of military live fire training that causes wildfires that can burn

unhindered, resulting in an array of fire-maintained ecosystems (Kalen et al. 2014). My additional field sites include both Piney Grove Preservation totaling approximately 1200 ha, and Big Woods Wildlife Management Area (hereafter BWPGC) totaling about 900 ha both in Sussex County, Virginia. Both sites are adjacent to Big Woods State Forest and contain mixed pine managed to promote an old-growth loblolly pine (*Pinus taeda*)-savanna forest ecosystem with an array of wildlife species such as red-cockaded woodpeckers (*Dryobates borealis*), bobwhite quail (*Colinus virginianus*), and wild turkey (*Meleagris gallopavo*). The BWPGC is located in the upper Coastal Plain physiographic province and contains one of the few remaining mature pine savannas in southeastern Virginia. In this area, prescribed burning is used as a management tool to maintain the rare pine savanna ecosystem to support a population of red-cockaded woodpeckers among other taxa (Watts and Harding 2007). The management goal for BWPGC is to maintain a fire return interval of 2-3 years (broad range 1-6 years) with prescribed burning implemented in the early growing season (April-May). Burning started with management of Red Cockaded Woodpecker habitat in 1999, now with about 95% of the area burned within a 2-3 fire-return interval (B. Clontz, the Nature Conservancy, pers. comm.)

The overall region containing Fort Barfoot and BWPGC are believed to be historically part of the southern fox squirrel range in the Piedmont and Coastal Plain regions in Virginia. The Piedmont, from the eastern ridges of the Blue Ridge Mountains to the Fall Line boundary with the Coastal Plain, contains rolling hills, a long history of land conversion to agriculture and pine plantation culture (Baker 2009, Fleming et al. 2017). Encompassing about 39% of the state, the Piedmont is mostly forested (61%)

with about 3% of palustrine wetlands, whereas the rest has been affected by agriculture, logging and urban/suburban development (VDCR 2016). The Coastal Plain or Tidewater region stretches roughly from Interstate 95 to the Atlantic Ocean, including the Delmarva Peninsula. This physiographic province can be characterized by a relatively flat to rolling landscape with geologic marine terraces, a diversity of wetland habitats, and remnants of longleaf pine and turkey oak (*Quercus laevis*) silvicultural stands of mixed pine, and mature remnant stands of mesic upland hardwoods (Fleming et al. 2017). Encompassing about 21% of the state, it has the greatest diversity of wetlands, with palustrine wetlands covering 22%, 46% forested, and about 9% developed (VDCR 2016). There is only somewhere around 13% of the Coastal Plain that is considered “unfragmented” and biologically intact (Weber 2007, VDCR 2016).

Virginia pine (*Pinus virginiana*) and tulip poplar (*Liriodendron tulipifera*) are early successional trees within upland forests resembling more of the Blue Ridge whereas the southern Piedmont contains shortleaf pine (*Pinus echinata*) and sweetgum with loblolly pine near the east and more resembles habitats of the Carolinas. The northern Coastal Plain is generally accepted to be north of the James River in Virginia (VDCR 2016). Whereas south of the James has a number of tree species largely restricted to the southern part of Virginia. Specifically, south of the James, forest communities include longleaf pine- oak (*Quercus spp.*) sandhills, pond pine (*Pinus serotina*) woodlands, loblolly pine forests and pocosins, bald cypress (*Taxodium distichum*) -tupelo (*Nyssa spp.*) swamps. North of the James, common vegetation types include drier oak-dominated forest, chestnut oak (*Quercus prinus*), American beech (*Fagus grandifolia*), mountain laurel (*Kalmia latifolia*) and loblolly pine. Many of these species located north of the James

River occur in wet, mesic conditions, with dense mid stories, and closed canopy cover.

Some authors characterize the forest types north of the James River as “southern mixed hardwood” since historically these types have not subjected natural fire as frequently as the southern Coastal Plain, which created these mesophytic conditions (VDCR 2016).

LITERATURE CITED

- Allen, A. W., Bernal, Y.K., and R. J. Moulton. 1996. Pine plantations and wildlife in the Southeastern United States: an assessment of impacts and opportunities. Information and Technology report 3. U.S. Department of Interior National Biological Service. Washington, D.C. 23 pp.
- Baker, J.C. 2009. Soils of Virginia. Pages 69-74 in Bran, D.E., Holshouser, D.L. and G. L. Mullins, editors. The Agronomy Handbook. Virginia Cooperative Extension, Blacksburg, Virginia.
- Edwards, J.W, Guynn, D.C, and M.R. Lennartz. 1989. Habitat use by southern fox squirrel in coastal South Carolina. Proceedings from Annual Conference SEAFWA 43: 337-345.
- Edwards, E. W., Heckel, D. G., and D. C. Guynn, Jr. 1998. Niche overlap in sympatric populations of fox and gray squirrels. The Journal of Wildlife Management 62(1): 354- 363.
- Edwards, J.W., Loeb, S.C., and D. C. Guynn, Jr. 1998. Use of multiple regression and use availability analyses in determining habitat selection by gray squirrels (*Sciurus carolinensis*). Pages 87-97 in M.A. Steele, Merritt, J.F. and D.A. Zegers, editors. Ecology and Evolutionary Biology of Tree Squirrels. Special Publication, Virginia Museum of Natural History, Martinsville, Virginia.
- Edwards, J.W. and J. Laerm. 2007. Eastern fox squirrel. Pages 410-416 in M. K. Trani-Griep, W.M. Ford, and B.R. Chapman, editors. The Land Manager's Guide to Mammals of the South. The Nature Conservancy, Durham, North Carolina.
- Emrick, Verl R, Matthew Fields, and Jessica Fitzpatrick. 2018. Removal, Propagation, and Transplantation of Michaux's Sumac (*Rhus michauxii*) Colonies from the Infantry Platoon Battle Course, Fort Pickett –Maneuver Training Center, 2018. Virginia Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University. VTCMI- Technical Report 05- 2018. Blacksburg, Virginia.
- Fish and Wildlife Service. 2015. Federal Register. Endangered and Threatened Wildlife and Plants: removal of the Delmarva Peninsula Fox Squirrel from the List of Endangered and Threatened Wildlife 80(220): 70700-70717.
- Fleming C.P., K.D. Patterson, and K. Taverna. 2017. The natural communities of Virginia: a classification of ecological community groups and community types. Third Approximation. Version 3.0. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Greene, D.U. and R. A. McCleery. 2017. Multi-scale responses of fox squirrels to land-

- use changes in Florida: Utilization mimics historic pine savannas. *Forest Ecology and Management* 391:42-51.
- Kalen, N.J., V.R. Emrick, R.M. Schneider, and M.J. St. Germain. 2014. Large and Meso mammal Camera Survey of Fort Pickett, Virginia. VTCMI-Technical Report-03-2014. Virginia Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University. Blacksburg, Virginia.
- Koprowski, J.L. 2005. Management and conservation of tree squirrels: the importance of endemism, species richness, and forest condition. USDA Forest Service Proceedings. RMRS-P-36. U.S. Department of Agriculture, Forest Service. Rocky Mountain Research Station, Fort Collins, Colorado.
- Loeb, S.C., and M.R. Lennartz. 1989. The fox squirrel (*Sciurus niger*) in southeastern pine-hardwood forests. Pages 142-147 in T.C. Waldrop, editor. Proceedings of pine-hardwood mixtures: a symposium on management and ecology of the type. United States Department of Agriculture. Forest Service, General Technical Report SE-58. Asheville, North Carolina.
- Martinuzzi, S., Withey, J.C., Pidgeon, A.M., Plantinga, A.J., McKerrow, A.J., Williams, S.G., Helmers, D.P, and V.C. Radeloff. Future land-use scenarios and the loss of wildlife habitats in the southeastern United States. *Ecological Applications* 25(1): 160-171.
- Prince, A., DePerno, C.S., Gardner, B., and C. E. Moorman. 2014. Survival and home-range size of southeastern fox squirrels in North Carolina. *Southeastern naturalist* 13(3): 456-462.
- Prince, A. P., Chitwood, M. C., Lashley, M.A., DePerno, C. S., and Moorman, C. E. 2016. Resource selection by southeastern fox squirrels in a fire-maintained forest system. *Journal of Mammalogy* 97(2): 631-638.
- Steele, M.A. and P. D. Weigl. 1992. Energetics and path use in the fox squirrel *Sciurus Niger*: responses to variation in prey profitability and path density. *The American Midland Naturalist* 128(1):156-167.
- Trani, M.K., Ford, W.M., Chapman, B.R., editors. 2007. The land manager's guide to mammals of the South. The Nature Conservancy, Durham, North Carolina.
- Virginia Department of Conservation and Recreation, Division of Natural Heritage. 2016. Overview of the physiography and vegetation of Virginia. Virginia Natural Heritage Program, Richmond, Virginia.
- Virginia Department of Wildlife Resources. 2015. Virginia's 204 Wildlife Action Plan. Virginia Department of Wildlife Resources, Henrico, Virginia.

- Virginia Department of Wildlife Resource (VADWR). 2023. Special Status Faunal Species in Virginia. Virginia Department of Wildlife Resources, Henrico, Virginia.
- Watts, B.D. and S. R. Harding. 2007. Virginia red-cockaded woodpecker conservation plan. Center of Conservation Biology Technical Report Series, CCBTR-07-07. College of William and Mary, Williamsburg, Virginia.
- Wear, D.N. and J.G. Greis, editors. 2002. Southern Forest Resource Assessment. General Technical Report SRS-53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- Weber, J.T. 2007. Virginia natural landscape assessment. 2007. Virginia Department of Conservation and Recreation, Division of Natural Heritage. GIS data, hardcopy and digital maps, and report. Accessed 11 July 2023 at http://dcr.virginia.gov/natura_heritage/vclnavnla.shtml.
- Whitaker, J.O and W. J. Hamilton. 1998. Mammals of the Eastern United States. Cornell University Press, Ithaca, New York.

Figure 1. Historical range of the southern fox squirrel (*Sciurus niger niger*) and other subspecies in North America derived from Edwards and Laerm (2007).

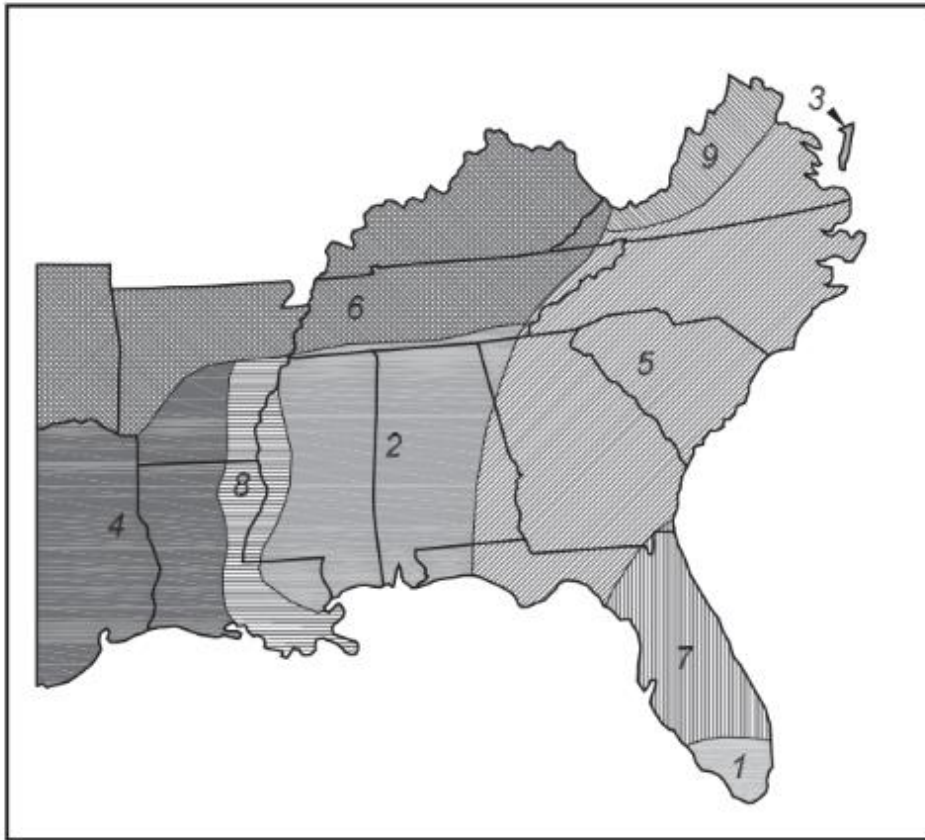
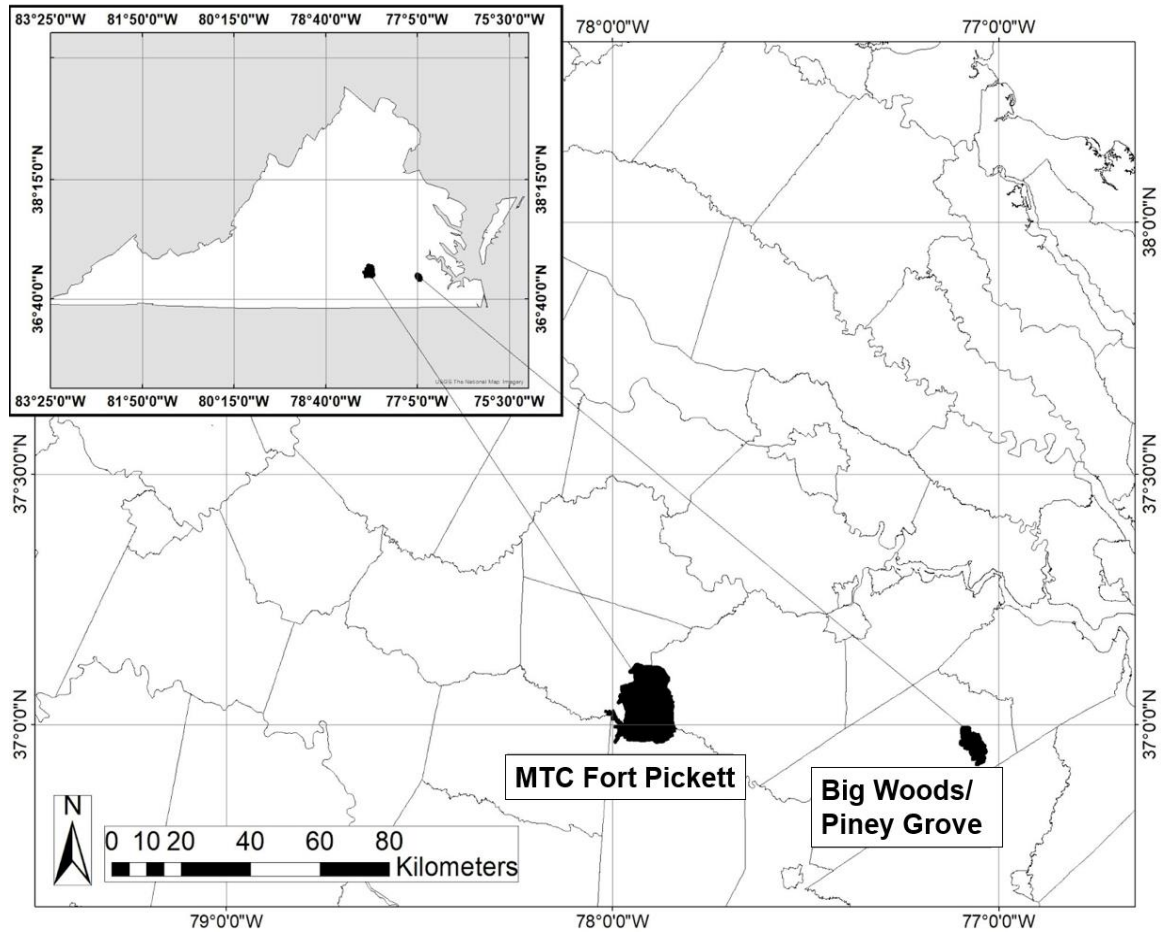


Figure 2. Distribution of *Sciurus niger* in the South:
(1) *S. n. avicennia*; (2) *S. n. bachmani*; (3) *S. n. cinereus*;
(4) *S. n. ludovicianus*; (5) *S. n. niger*; (6) *S. n. rufiventer*;
(7) *S. n. shermani*; (8) *S. n. subauratus*; (9) *S. n. vulpinus*.

Figure 2. Southeastern fox squirrel (*Sciurus niger niger*) field sites 2019–2022: Military Training Center Fort Barfoot, Nottoway County, Virginia (left) in the Piedmont region and the Virginia Department of Wildlife Resources’ Big Woods Wildlife Management Area and Nature Conservancy’s Piney Grove in Sussex County (right) in the Coastal Plain region.



Chapter II. Resource selection of the Southern Fox Squirrel (*Sciurus niger niger*) in the Piedmont and Coastal Plain of Virginia

INTRODUCTION

A species home range estimation can provide data including but not limited to population densities, foraging behavior, distribution of resources, and habitat selection that can further provide informed management actions (Harris et al. 1990). Fox squirrel home ranges have been poorly studied across all subspecies (Conner 2000). In fact, little to no data exists regarding fox squirrels in the Southeast, particularly when they were once abundant. Nonetheless, for a species of management concern, and because studies in other southeastern states may not be directly transferable in southeastern Virginia, it is important to understand habitat use characteristics of southern fox squirrels (Perkins and Conner 2004).

Because home range and habitat use are affected by multiple factors, there is a need for research in order to appropriately manage these species (Conner 2000). Further, the home range size and composition of a home range can be very telling for a species. The size of the home range not only reflects life history and behavioral traits as well as transferability to different areas (Don 1983), but it also relates to the habitat quality of an area. In terms of resource selection, a smaller home range would indicate that a species is likely receiving all the food space, and/or nesting requirements that they need in that area of use so there is no need to venture further. Whereas the larger the home range, the greater the distance a species needs to utilize to get the necessary habitat requirements. This therefore reflects on the quality and quantity of appropriate habitat for a species in a

particular area (Mitchell and Powell 2004).

Specifically, in Virginia, home range estimates for the Delmarva fox squirrel were found to be 2.5 hectares for female individuals and 6.1 hectares for males using the modified minimum-area method (Edwards et al. 2003). While there is home range analysis and habitat use information for the Delmarva fox squirrel, data on southern fox squirrels does not exist for Virginia. Conversely, fox squirrels (*S. n. ludovicianus*) in east Texas, Florida (*S. n. shermani*), and Georgia and North Carolina (*S. n. niger*) in have been found to have larger home ranges than the eastern fox squirrel (*S. n. vulpinus*) in the Midwest (Koprowski 1994). In addition, male fox squirrels have significantly larger home ranges than female fox squirrels (Conner 2000, Perkins and Conner 2004, Prince et al. 2014). Home ranges for southern fox squirrels in South Carolina reflected a high probability of presence in integrated pine-hardwood edges suggesting the importance of pine-hardwoods ecotones (Edwards et al. 1989). Southern fox squirrel home ranges in Georgia were similar to findings from South Carolina, with home range preferences in mixed pine-hardwood forests, as well as mature pine forests (Perkins and Conner 2004).

Live trapping and radio tracking of southern fox squirrels is a useful method to identify finer scale habitat preferences. However, due to their highly variable movements and behavioral responses, live capture can be difficult (Greene et al. 2016). On a pine savanna ecosystem similarly managed to Big Woods Wildlife Management Area and Pinery Grove Complex (BWPGC) with heavy reliance on fire as a silvicultural tool, southern fox squirrels displayed considerable seasonal changes in activity levels and home-range size. Spring and Fall were typically periods of higher movement and activity, due to increased foraging, and home ranges for both males and females were both

greatest in the spring (Prince et al. 2014). Additionally, home range estimates in the Coastal Plain of South Carolina revealed southern fox squirrels selected habitats with a mixed forest composition and short return interval prescribed burns (1-3 years; Prince 2013).

The objective of my live capture study was to investigate the fine scale habitat use variables that southern fox squirrels select in the Coastal Plain region of Virginia. Through camera trapping analysis, nest box monitoring, live capture studies, and opportunistic observations from all personnel on the base, no southern fox squirrels were identified at our Piedmont field site at Fort Barfoot. Therefore, live capture and tracking studies were solely conducted at the Coastal Plain field site, BWPGC. I predicted home range and resource selection findings to reflect larger home ranges for males and smaller home ranges for females as it has been found in other studies across the southeast (Table 1). I also predicted that southern fox squirrels will select of pine-hardwood areas that are burned frequently at both the core use and landscape use levels. Further, I think home range estimates will be larger than their home ranges found elsewhere in the Southeast indicating a further need for habitat creation and management.

METHODS

Live Capture

I focused on live trapping on BWPGC in locations where fox squirrels have occurred most often on remote cameras as well from opportunistic field observations. Prior to live capture, I deployed trail cameras in random transects (Bushnell Trophy HD cameras, Bushnell Outdoor Products, Overland, KS) at Fort Barfoot and BWPGC to initially assess the presence of southern fox squirrels following the methods of Tye et al.

(2015) and Greene and McCleery (2017). Each camera was placed 250m from the next camera site and each transect was a total 1000 m in length. Opportunistic observations were any areas identified to be used by fox squirrels that I saw while in the field or from personnel on the field site. For live capture, I deployed model 103 Tomahawk traps (48.26 cm length x 15.24 cm width x 15.24 cm height; Tomahawk Live Traps, Hazelhurst, WI), wooden-box traps (Baumgartner 1940) and also captured individuals from previously established nesting boxes (McCleery et al. 2007, Bosson et al. 2013). Wire cage tomahawk traps and box traps were deployed in grids of 3 X 4 with distance of 25-50 meters in between traps (Herbers and Klenner 2007). Within grid deployments, I attached the half of the traps to trees using bungee cords, as well as on down trees (Huggins and Gee 1995). The traps attached to trees were positioned with the opening at the approximate center of the tree to aid ease of access. I baited each trap with whole kernel corn and left a small trail of corn leading into the trap (Prince et al. 2016, Greene and McCleery 2017, Amspacher et al. 2019).

In addition to the trap grids, I strategically placed 10-15 traps around the nesting trees with observed drey nests to increase targeted individual capture (Greene and McCleery 2017). Initially, to entice squirrels and to allow squirrels to become comfortable with traps, I baited traps, zip-tied them open, and left them open 24 hours for a period of one week (McCleery et al. 2007). After the acclimatization period, I opened traps in the morning around sunrise, checked them late-morning/early afternoon, and then checked them once more before I closed them overnight in case of accidental captures of nocturnal animals (Huggins and Gee 1995).

To also collect individuals for capture, I checked nest boxes for southern fox squirrel presence before sunrise, during mid-day, and after sunset (Edwards et al. 1998). I also checked tree nest boxes during cold, rainy, or snowy weather events as southern fox squirrels tend to use nesting boxes for cover and refuge during inclement weather (Nixon et al. 1984). Monitoring of nest boxes was performed with a wireless cavity inspection camera (Version 3.3, IBWO, David Luneau, Arkansas) to identify the presence of any squirrels. The use of small-scale cameras on pole apparatuses to check nest boxes is a lightweight, cost-effective, efficient, and discrete method of monitoring (Richardson et al. 1999). When a squirrel was present, I plugged the opening to the nest box, and removed the box from the tree, and used a live handling bag and bite-resistant gloves to entice the squirrel out of the box for measurements (Dimmik and Pelton 1994, Perkins and Conner 2007, Lee et al. 2009). The handling bag method was also used for capturing southern fox squirrels from wire traps and box traps. I recorded the sex (based on Weigl et al. 1989), weight, age (juvenile or adult), ear length, hind foot length, and general body condition. I also attached a 1 Monel fingerling ear tag (Conner 2001, McCleery et al. 2010, Prince et al. 2016). Trapping and handling followed guidelines provided by the Virginia Tech Institutional Animal Care and Use Committee permit #20-039.

Tracking and Telemetry

I fit each captured fox squirrel individual with a VHF radio collar (Holohil, model PD-2C radio collars, Holohil Systems Limited, Ontario, Canada). The collar was fit to be tight enough so that only the end of a mechanical pencil can fit between the neck and the collar. Proper sizing ensured that the collar stayed on through the squirrel's daily activities without becoming a nuisance or hurting the squirrel (Silvy et al. 2005). Once

released, squirrels were located via biangulation (Perkins and Conner 2007). Using a 3-element yagi antenna, I estimated telemetry error by placing collars on down trees and on top of nest boxes in trees in an attempt to capture the landscape use on the ground and in trees by southern fox squirrels. Telemetry error aimed at collars on the ground was 5° (SE=0.84) with a mean distance from transmitter location to receiving location of 259.04 m (SE= 57.30, $N = 15$). Telemetry error in trees was 8° (SE=1.1) with a mean distance from transmitter location to receiving locations of 228.09 m (SE=48.73, $N=17$; White and Garrott 1990). I tracked each squirrel at random intervals throughout each day over a 12–14-hour period. Squirrels were located at least twice a week between sunrise and sunset during 1-2 hours tracking bouts with locations collected every 5 minutes from distinct locations (Prince et al. 2016). All squirrels captured were tracked until collar failure or predation to ensure a robust dataset (McCleery et al. 2007). Additionally, to locate dens and leaf nests, I used homing methods to identify overnight den trees before and after sunset, and during mid-day loafing periods (Ford et al. 2014).

Statistical Analysis

Initial mapping of points and biangulation stations were loaded in LOCATE III (Pacer Co., Truro, Nova Scotia, Canada). The rest of my analyses was performed using R version 4.2.2 (R Core Team, 2022). Using the *adehabitat* package in R (Calenge and Fortmann-Roe 2023) I identified the 50% and 95% adaptive kernel density estimates (KDE) for each individual fox squirrel to identify home range size differences for males and females (Ford et al. 2014). To examine resource selection by southern fox squirrels, I focused on identifying the second and third-order habitat selection collectively from our captured individuals (Johnson 1980). Due to my smaller sample size as well as size of

each adaptive kernel home range, third order habitat selection was calculated from “used” areas using the established native points within the 50% (core use area) adaptive kernel home range. I then compared the native points to “available” areas which I considered randomly placed points in the 95% adaptive kernel home range (more broad, approximately entire home range). For second order selection, I considered “used” as points randomly placed within the 95% adaptive kernel home range. I then compared those random points to the “available” or landscape area in which I randomly placed points on the study site that was buffered by the radius of southern fox squirrel range at 700m (Kroeger et al. 2020, Dawson et al. 2009).

Resource selection function predictions and modeling were performed with generalized linear models (GLM) using the stats package (R studio, Ver. 3.6.2). I established 8 *a priori* candidate models by examining covariates that could explain habitat selection by southern fox squirrels at BWPGC and surrounding landscape (Table 2, Table 3). Covariates influencing resource selection were, basal area, canopy cover, number of prescribed burns since 2019, time since last prescribed burn (in years), fragmentation, and savanna cover type (Table 4). I considered these variables as they would be directly related to forest succession and vegetation structure useful for further predictive efforts across the larger landscape (Hayes et al. 1981, Deuser 1988). The presence of savanna habitat (1 as savanna; 0 as other cover types) was considered as a covariate as BWPGC is dominated by loblolly pine woodland savannas. I reclassified landcover to savanna or not savanna by creating a supervised classification ensemble model from known areas of savanna on the landscape using a vegetation height layer (heights > 18 m; LANDFIRE 2022) and percent evergreen forest derived from the

National Land Cover Database, 2019 release (> 90% evergreen forest; Dewitz and USGS, 2022). I then cut predictions based on a threshold that maximized sensitivity and specificity in relation to the training point classifications.

To account for collinearity among our covariates, I used the package *usdm* (Naimi 2017) where any variables that tested above 0.7 in correlation were not included in the final model analysis (Amspacher et al. 2019) and used the *MuMIn* package in R (Bartón 2020) to perform a model selection that ranks models by our chosen AICc criteria (Boone et al. 2017). Using Akaike's Information Criteria for small sample sizes (AICc), I considered models within 2 AICc units of the top models to be competing models (Sovie et al. 2020, Burnham and Anderson 2002). Of the covariates in our top models, I considered covariates with 95% confidence intervals (CI) not crossing zero to be significant predictors of resource selection (Shake et al. 2011, Bowling et al. 2014).

RESULTS

From January to April 2022, I captured four individual southern fox squirrels: two males and two females (Table 5). All southern fox squirrels were captured out of previously established nest boxes since I had no success in capturing squirrels out of box traps. We tracked each fox squirrel until collar failure and collected 70-100 points per individual based on date captured. Through tracking, we attempted to sample each squirrel at even intervals to emphasize selection during the day, as well as identifying nesting locations during the evening and loafing locations during midday. However, during the winter months, southern fox squirrels tended to have more unimodal activity and therefore I attempted to sample each individual at all intervals of daytime activity. For home range estimates, the average 95% adaptive kernel home range for males was

176.49 ha (SE = 25.73, N = 2) and the average 50% adaptive kernel home range for males was 40.62 ha (SE = 5.87 N = 2). For females, the average 95% adaptive kernel home range was 28.51 ha (SE = 0.485, N = 2) and the average 50% adaptive kernel home range was 4.71 ha (SE = 0.34, N = 2). In total, I located the captured squirrels for a total of 378 locations across all four seasons during 2022 and each adaptive kernel home range rarely overlapped (Figure 3).

Model selection from 8 *a priori* candidate models reflected that the top model for second order habitat selection was the savanna and number of burns covariates. Southern fox squirrel probability of use increased with the savanna cover type ($\beta = 2.095$, SE = 0.158) and with increasing number of burns since 2019 ($\beta = 1.24$, SE = 0.098; Figure 4). The top model for third order habitat selection was also the savanna covariate, but in relation with the time since the last prescribed burn (in years) covariate. Southern fox squirrel probability of use increased with the savanna cover type ($\beta = 0.799$, SE = 0.214) and decreased with increasing time since prescribed burns ($\beta = -0.233$, SE = 0.097; Figure 5).

DISCUSSION

The home range size estimation of southern fox squirrels at BWPGC largely followed other Coastal Plain region trends in that male home ranges were larger than female home ranges as I predicted. In previous studies, males have been found to move outside of their utilization areas, or individual home ranges, as females typically stay within the same areas and rarely move across those larger distances, mirroring the difference in sizes of male and female home ranges especially during mating season (Don 1983). I also found this to be true as I tracked males and females throughout their mating

seasons. Home range sizes generally fell within the reported ranges of other studies in North Carolina, South Carolina, and Georgia Coastal Plain; however, they are on the larger end of that gradient compared to some other studies (Table 1). This may point to the fact that although there is suitable habitat, there may be specific limiting landscape characteristics such as use of hardwood areas that are driving large home ranges as we predicted. However, home range size and shape have less ecological significance than does where their ranges are, and why they are using these areas (Sanderson 1966).

Resource selection of southern fox squirrels according to my second and third habitat selection analysis reflected the importance of savanna cover types and not only the rotation of which prescribed burns are performed at the local and landscape scale, but also the frequency of which the prescribed burns. The greater frequency that an area is burned, the probability that southern fox squirrels will use that area increases. In other words, for every unit increase in burn frequency, southern fox squirrel probability of use increases by 1.24. Further, for every unit increase in years since the last prescribed burn, southern fox squirrel probability of use decreases by 0.28. Prescribed burning maintains open forest conditions that southern fox squirrels require (Prince et al. 2016, Robbins and Meyer 2022) preventing the shift from open forest dynamics, via fire suppression and site mesophication, to less suitable closed-canopy forests (Nowacki and Abrams 2008). Furthermore, southern fox squirrels by choosing areas that are burned more frequently decreases visual hindrance of other vegetation, which helps predator avoidance (Boone et al. 2017).

The selection for the savanna cover type over other cover types was intriguing as my reclassification of land cover as 'savanna' or 'other' was calculated specifically from

tree height (Conner and Godbois 2003) and the evergreen cover type from the 2019 National Land Cover Database. At BWPGC, evergreen stands include a majority of loblolly pine, along with small percentages of shortleaf pine and longleaf pine. Selection of the savanna covariate was interesting since southern fox squirrels in other studies choose of mixed pine-hardwood habitat and hardwood patches because southern fox squirrels use mature hardwood trees for food, cover, and nesting (Loeb and Lennartz 1989, Conner and Godbois 2003, Trani et al. 2007, Prince et al. 2016). However, southern fox squirrels can still establish stable populations in pine-dominated habitat as they supplement part of their diet with pine seeds, including those from loblolly pine (Appendix C, Figure C.2; Loeb and Lennartz 1989, Asaro et al 2003, Trani et al. 2007).

Capture success aligns with previous studies revealing that live trapping fox squirrels has been substantially difficult due to fox squirrels' often low local abundance resulting in poor capture success and high trap-night requirements (Weigl et al. 1989, Green and McCleery 2017). The scope of this study was slightly limiting in that only four individuals were captured throughout live trapping. Therefore, larger sample sizes could have the ability to slightly change our home range findings. However, to caveat this, I was able to track these squirrels for >50 points per individual at a minimum to help overcome this potential sampling bias. Further, I considered 'available' habitat to be all of BWPGC buffered by a biologically meaningful distance of 700m as that is the typical radius of a southern fox squirrel range. However, this definition of availability may not fully capture the surrounding area that is available to southern fox squirrels at BWPGC. In efforts to control these biases, it was necessary to base live capture as well as available points at random locations.

Southern fox squirrel populations appear to be selecting areas of BWPGC specifically managed for open woodland/savanna areas and maintained by prescribed burning. However, my data also indicates that southern fox squirrels are choosing pine dominated savannas instead of pine-hardwood mixes or hardwood habitat unlike other parts in their range. Selection of pine dominated savannas could be due to the fact that hardwood-dominated habitat at BWPGC is typically closed canopy with considerable mid-story shrub species (Gilliam and Platt 1999, Sovie et al. 2021). These habitats tend to favor gray squirrels over southern fox squirrels due to interspecific competition (Sovie et al. 2021). Therefore, my study suggests that 1) successful southern fox squirrel habitat management should involve frequent prescribed burns focused in pine dominated savanna; and 2) further investigations should evaluate resource partitioning and competitive exclusion of southern fox squirrels and gray squirrels in varying habitat.

LITERATURE CITED

- Ampacher, K. 2018. Southern fox squirrel (*Sciurus niger niger*) translocation, occupancy, and foraging behaviors. Thesis, Marshall University, Huntington, West Virginia, USA.
- Ampacher, K., B. Bauer, J. Waldron, E. Wiggers, and S. Welch. *Sciurus niger niger* (southern fox squirrel) density and the diurnal patterns, occupancy, and detection of sympatric southern fox squirrels and *S. carolinensis* (eastern gray squirrels) on Spring Island, South Carolina. *Southeastern Naturalist* 18(2): 321-333.
- Asaro, C., S. C. Loeb, and J. L. Hanula. 2003. Cone consumption by southeastern fox squirrels: a potential basis for clonal preferences in a loblolly and slash pine seed orchard. *Forest Ecology and Management* 186(1-3): 185-195.
- Bartoń, k. 2020. MuMIn: Multi-Model Inference. R Package Version 1.47.5. <<https://cran.r-project.org/web/packages/MuMIn/index.html>>. Accessed 2 May 2023.
- Baumgartner, L.L. 1940. Trapping, handling, and marking fox squirrels. *The Journal of Wildlife Management* 4(4): 440- 450.
- Boone, W. W., R. A. McCleery, and B. E. Reichert. 2017. Fox squirrel response to forest restoration treatments in longleaf pine. *Journal of Mammalogy* 98(6):1594-1603.
- Bosson, C.O., Palme, R., and R. Boonstra. 2013. Assessing the impact of live-capture, confinement, and translocation on stress and fate in eastern gray squirrels. *Journal of Mammalogy* 94(6): 1401-1411.
- Bowling, S. A., C. E. Moorman, C. S. Deperno, and B. Gardner. 2014. Influence of landscape composition on northern bobwhite population response to field border establishment. *The Journal of Wildlife Management* 78(1):93-100.
- Burnham, K.P. and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach* (2nd Edition). Springer-Verlag, New York, New York.
- Calenge, C and S. Fortmann-Roe. 2023. AdeHabitat: Home Range Estimation. R Package Version 0.4.12. <<https://cran.r-project.org/web/packages/adeHabitatHR/index.html>>. Accessed 21 April 2023.
- Conner, L. M. 2000. Home range sizes of fox squirrels in Southwest Georgia. *Proceedings of the Annual Conference for the Southeastern Association of Fish and Wildlife Agencies* 54: 400-406.
- Conner, L.M. 2001. Survival and cause-specific mortality of adult fox squirrels in southwestern Georgia. *The Journal of Wildlife Management* 65(2):200-204.

- Conner, L.M. and I. A. Godbois. 2003. Habitat associated with daytime refugia of fox squirrels in a longleaf pine forest. *The American Midland Naturalist* 150(1): 123-139.
- Dawson, R. D., J.C. Lee, D. A. Osborn, and K. V. Miller. 2009. Survival, movements and habitat use of translocated southern fox squirrels. *American Midland Naturalist* 162(2):335-345.
- Dimmick, R.W. and M. R. Pelton. 1994. Criteria and Sex and Age. Pages 169-214 in T. A. Bookhout, editor. *Research and Management Techniques for Wildlife and Habitats*, Fifth Edition. The Wildlife Society, Bethesda, Maryland.
- Don, B.A.C. 1983. Home range characteristics and correlates in tree squirrels. *Mammal Review* 13(2/3/4): 123-132.
- Edwards, J.W., D. C. Guynn, Jr., and M. R. Lennartz. 1986. Habitat use by southern fox squirrel in coastal South Carolina. *Proceedings of the Annual Conference for the Southeastern Association of Fish and Wildlife Agencies* 43: 337-345.
- Edwards, J. W., D. C. Guynn, and M. R. Lennartz. 1989. Habitat use by southern fox squirrels in coastal South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 42:337-345.
- Edwards, J.W., D. G. Heckel, and D. C. Guynn Jr. 1998. Niche Overlap in Sympatric Populations of Fox and Gray Squirrels. *The Journal of Wildlife Management* 62(1): 354-363.
- Edwards, J.W., Ford, W.M, and G. Guynn. 2003. Fox and Gray Squirrels. Pages 248-267 in Feldhamer, G.A., Thompson, B.C., and J.A. Chapman, editors *Wild mammals of North America: Biology, Management, and Conservation*. Johns Hopkins University Press, Baltimore, Maryland.
- Edwards, J.W. and J. Laerm. 2007. Eastern fox squirrel. Pages 410-416 in M. K. Trani-Griep, W.M. Ford, and B.R. Chapman, editors. *The Land Manager's Guide to Mammals of the South*. The Nature Conservancy, Durham, North Carolina.
- Ford, W.M., C. A. Kelly, J.L. Radrigue, R. H. Odom, D. Newcomb, L. M. Gilley, and C. A. Diggins. 2014. Late winter and early spring home range and habitat use of the endangered Carolina northern flying squirrel in western North Carolina. *Endangered Species Research* 23: 73-82.
- Gilliam, F.S. and W.J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. *Plant Ecology* 140(1): 15-26.
- Greene, D. U., R. A. McCleery, L. M. Wagner, and E. P. Garrison. 2016. A comparison of four survey methods for detecting fox squirrels in the southeastern United States. *Journal of Fish and Wildlife Management* 7(1):99-106.

- Greene, D.U. and R. A. McCleery. 2017. Multi-scale responses of fox squirrels to land-use changes in Florida: Utilization mimics historic pine savannas. *Forest Ecology and Management* 391:42-51.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., and S. Wray. 1990. Home-range analysis using radio-tracking data-a review of problems and techniques particularly as applied to the study of animals. *Mammal Review* 20(2/3): 97-123.
- Herbers, J. and W. Klenner. Effects of logging pattern and intensity on squirrel demography. *Journal of Wildlife Management* 71(8): 2655-2663.
- Hilliard, T. H. 1979. Radio-telemetry of fox squirrels in the Georgia coastal plain. Thesis, University of Georgia, Athens, USA.
- Huggins, J.G., and K.L. Gee. 1995. Efficiency and selectivity of cage trap sets for gray and fox squirrels. *Wildlife Society Bulletin* 23(2): 204-207.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluation resource preference. *Ecology* 61:65-71.
- Koprowski, J. 2005. The response of tree squirrels to fragmentation: A review and synthesis. *Animal Conservation Forum* 8(4): 369-376.
- Koprowski, J.L. 1994. *Sciurus niger*. *The American Society of Mammalogists* 479: 1-9.
- Kroeger, A.J., C. S. DePerno, C.A. Harper, S. B. Rosche, and C. E. Moorman. 2020. Northern bobwhite non-breeding habitat selection in a longleaf pine woodland. *The Journal of Wildlife Management* 84(7): 1348- 1360.
- LANDFIRE. 2022. Fuel vegetation height layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed 12 May 2023 at <http://www.landfire/viewer>.
- Lee, J.C., D. A. Osborn, K.V. Miller. 2009. Habitat use by a dense population of southern fox squirrels. *Southeastern Naturalist* 8(1): 157-166.
- Loeb, S. C. and M. R. Lennartz. 1989. The fox squirrel (*Sciurus niger*) in Southeastern pine-hardwood forests. Pages 142-145 in T. A. Waldrop, editor. *Proceedings of Pine-Hardwood Mixtures. A Symposium on Management and Ecology of the Type*. Southeastern Forest Experiment Stat, Asheville, North Carolina.
- MacKenzie, D.I, Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. and J.E. Hines. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, Burlington, Massachusetts.
- McCleery, R. A., Lopez, R. R., N. J. Silvy, and D. L. Gallant. 2007. Fox squirrel survival in urban and rural environments. *The Journal of Wildlife Management* 71(1): 133-137.

- McCleery, R.A. R. R. Lopez, N.J. Silvy, and D. L. Gallant. 2010. Fox squirrel survival in urban and rural environments. *The Journal of Wildlife Management* 72(1): 133-137.
- Mitchell, M.S. and R. A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* 177(1-2): 209-232.
- Naimi, B. 2017. Usdm: Uncertainty Analysis of Species Distribution Models. Version 1.1-18. <<https://cran.r-project.org/web/packages/usdm>>. Accessed 6 October 2022.
- Nixon, C.M, Harvera, S.P. and L.P. Hansen. 1984. Effects of nest boxes on fox squirrel demography, condition and shelter use. *The American Midland Naturalist* 112(1):157- 171.
- Nowacki, G. J. and M. D. Abrams. 2008. The demise of fire and “mesophication” for forests in the eastern United States. *BioScience* 58(2): 123-138.
- Perkins, M.W. and L.M. Conner. 2004. Habitat use of fox squirrels in Southwestern Georgia. *Journal of Wildlife Management* 68(3): 509-513.
- Prince, A., DePerno, C.S., Gardner, B., and C.E. Moorman. 2014. Survival and home-range size of southeastern fox squirrels in North Carolina. *Southeastern Naturalist* 13(3): 456-462.
- Prince, A. P., Chitwood, M. C., Lashley, M.A., DePerno, C. S., and Moorman, C. E. 2016. Resource selection by southeastern fox squirrels in a fire-maintained forest system. *Journal of Mammalogy* 97(2): 631-638.
- Prince, A. 2013. Habitat selection, survival and home range size of the southeastern fox squirrel. M.S. Thesis. North Carolina State University, Raleigh, North Carolina, USA.
- Richardson, D.M., Bradford, J.W., Range, P.G., and J. Christensen. 1999. A video probe system to inspect red-cockaded woodpecker cavities. *Wildlife Society Bulletin* 27(2): 353-356.
- Robbins, L. E. and R. L. Meyers. 1992. Seasonal effects of prescribed burning in Florida: a review. Tall Timbers Research Station, Miscellaneous Publication 8, Tallahassee, Florida.
- Sanderson, G. C. 1966. The study of mammal movements-a review. *Wildlife Management* 30:215-235.
- Shake, S. C., C. E. Moorman, and M. R. Burchell II. 2011. Cropland edge, forest succession, and landscape affect shrubland bird nest predation. *The Journal of Wildlife Management* 75(40): 825-835.

- Silvy, N.J., Lopez, R.R., and M.J. Peterson. 2005. Wildlife Marking Techniques. Pages 339-376 in C. E. Braun, editors. Techniques for wildlife investigations and management. The Wildlife Society, Bethesda, Maryland.
- Sovie, A. R., Greene, D.U., and R. A. McCleery. 2020. Woody cover mediates fox and gray squirrel interactions. *Frontiers in Ecology and Evolution* 8(239): 1-10.
- Sovie, A.R., L. M. Conner, J. S. Brown, and R. A. McCleery. 2021. Increasing woody cover facilitates competitive exclusion of a savanna specialist. *Biological Conservation* 255:1-8.
- Shepherd, F. B. and R. K. Swihart. 1995. Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. *Canadian Journal of Zoology* 73(11): 2098-2015.
- Weigl, P.D., Steele, M.A., Sherman, L.J, Ha, J.C, and T.L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. Bulletin-Tall Timbers Research Station, Tallahassee, Florida.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., London, United Kingdom.

Table 1. Comparison of southern fox squirrel home ranges in the U.S. Coastal Plain regions of North Carolina, South Carolina, Georgia, and Virginia.

Location	Average Male (ha)	Average Female (ha)	Source
Fort Bragg, NC ^a	81.26 ± 16.4	19.83 ± 14.12	Prince et al. 2014
Southeastern NC ^c	26.6	17.2	Weigl et al. 1989
Parris Island, SC ^b	49.7 ± 16.4	6.6 ± 1.2	Amspacher et al. 2018
Spring Island, SC ^e	9.57 ± 3.56	3.43 ± 0.65	Lee et al. 2008
Georgetown, SC ^d	31.5	19.3	Edwards et al. 1986
St. Phillips Island, SC ^c	45.4 ± 12.91	36.67 ± 7.23	Dawson et al. 2009
Hall Island, SC ^c	124.2 ± 21	30.67 ± 9.06	Dawson et al. 2009
Ichauway, GA ^d	37.0 ± 3.6	21.0 ± 6.3	Conner 2000
Big Woods/Piney Grove Preservation, VA ^e	176.49 ± 25.73	28.51 ± 0.48	<i>Current Study</i>

a=99% kernel-density, b=85% minimum convex polygon, c=100% minimum convex polygon, d=95% kernel-density, e=95% adaptive kernel-density

Table 2. Second Order Habitat Selection. Southern fox squirrel (*Sciurus niger niger*) resource selection *a priori* models on the Virginia Department of Wildlife Resources’ Big Woods Wildlife Management Area and Nature Conservancy’s Piney Grove in Sussex County, Virginia, 2022. Models considered as having strong empirical support at $\Delta AICc < 2.0$ from the top model. Savanna = Presence of savanna cover type or other cover type. Number of burns= Number of burns since 2019. Fragmentation= Degree of forest fragmentation. Canopy Cover = percent canopy closure. Basal Area = basal area in ha².

Model	AICc	$\Delta AICc$	Model Wt.
Savanna + Number of Burns	1117.5	0.00	0.911
Number of Burns + Fragmentation	1122.2	4.65	0.089
Number of Burns	1309.4	191.85	0.000
Savanna	1311.0	193.46	0.000
Fragmentation	1328.3	210.76	0.000
Canopy Cover + Basal Area	1685.1	567.62	0.000
Canopy Cover	1689.5	571.99	0.000
Basal Area	1707.1	589.60	0.000

Table 3. Third Order Habitat Selection. Southern fox squirrel (*Sciurus niger niger*) resource selection *a priori* models on the Virginia Department of Wildlife Resources’ Big Woods Wildlife Management Area and Nature Conservancy’s Piney Grove in Sussex County, Virginia, 2022. Models considered as having strong empirical support at $\Delta AICc < 2.0$ from the top model. Savanna = Presence of savanna cover type or other cover type. Number of burns= Number of burns since 2019. Fragmentation= Degree of forest fragmentation. Canopy Cover = percent canopy closure. Basal Area = basal area in ha².

Model	AICc	$\Delta AICc$	Model Wt.
Savanna + Time Since Burn	869.7	0.00	0.807
Savanna	873.5	3.74	0.124
Fragmentation + Savanna	875.5	5.82	0.044
Fragmentation	877.1	7.35	0.020
Basal Area	882.0	12.31	0.002
Time Since Burn	882.3	13.53	0.002
Canopy Cover + Basal Area	883.6	13.90	0.001
Canopy Cover	885.6	15.90	0.000

Table 4. Covariates for habitat use vs. habitat availability for southern fox squirrels (*Sciurus niger niger*) on the Virginia Department of Wildlife Resources’ Big Woods Wildlife Management Area and Nature Conservancy’s Piney Grove in Sussex County, Virginia, 2022.

Covariate	Description	Objective of Covariate
Canopy Cover	Canopy closure percentage	Percent canopy cover was derived from on-site measurements using a concave spherical densiometer (Lemmon, 1957). Our goal is to capture fine scale differences between hardwood dominant areas and pine dominant areas that might affect fox squirrel and gray squirrel site selection (Greene and McCleery 2017).
Basal Area	Cross sectional area of trees at diameter at breast height (DBH) in m ² /ha	Basal area was calculated in the field with a 10 basal area factor prism. Basal area of each location was calculated to demonstrate surrounding forest structure density (Hayes et al. 1981).
Fragmentation	Reclassification of forested areas in 6 different categories: patch forest, edge forest, perforated forest, small core forest, medium core forest, and large core forest (UCONN 2023).	Fragmentation refers to areas of the forest that are continuous swaths or smaller abrupt patches and edges. Fox squirrels have been known to be affected by patch size and negatively impacted by fragmentation (Koprowski 2005, Shepherd and Swihart 1995).
Savanna	The presence of the savanna cover type denoted by “1” and all other cover types denoted by “0”	Savanna was derived from reclassified landcover to savanna or not savanna by creating a supervised classification ensemble model from known areas of savanna on the landscape using a vegetation height layer (LANDFIRE 2022) and percent evergreen forest derived from the National Land Cover Database, 2019 release (Dewitz and USGS, 2022). I then cut predictions based on a threshold that maximizes sensitivity and specificity in relation to the training point classifications. Savanna was used as a covariate as savanna

woodlands have been known to be the preferred habitat of fox squirrels (Edwards et al. 2003).

Number of Burns

The number of prescribed burns completed on the study site from 2019 until fox squirrel capture and tracking in 2022.

The number of burns speaks upon the frequency at which prescribed burns are managed on the study site. It is important as it has been deemed an important management tool for fox squirrel habitat in other parts of their range (Conner et al. 1999).

Table 5. 95% adaptive kernel home ranges for individual captured southern fox squirrels (*Sciurus niger niger*) by sex on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2022.

Date of Capture	Capture Time	Sex	95% KDE (ha)	50% KDE (ha)
2/8/2022	13:30	Female	28.02	5.05
2/17/2022	7:28	Female	28.99	4.37
3/31/2022	9:35	Male	150.76	34.75
4/15/2022	7:55	Male	202.21	46.49

Figure 3. 95% and 50% adaptive kernel density estimates for four individually captured southern fox squirrels (*Sciurus niger niger*) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2022.

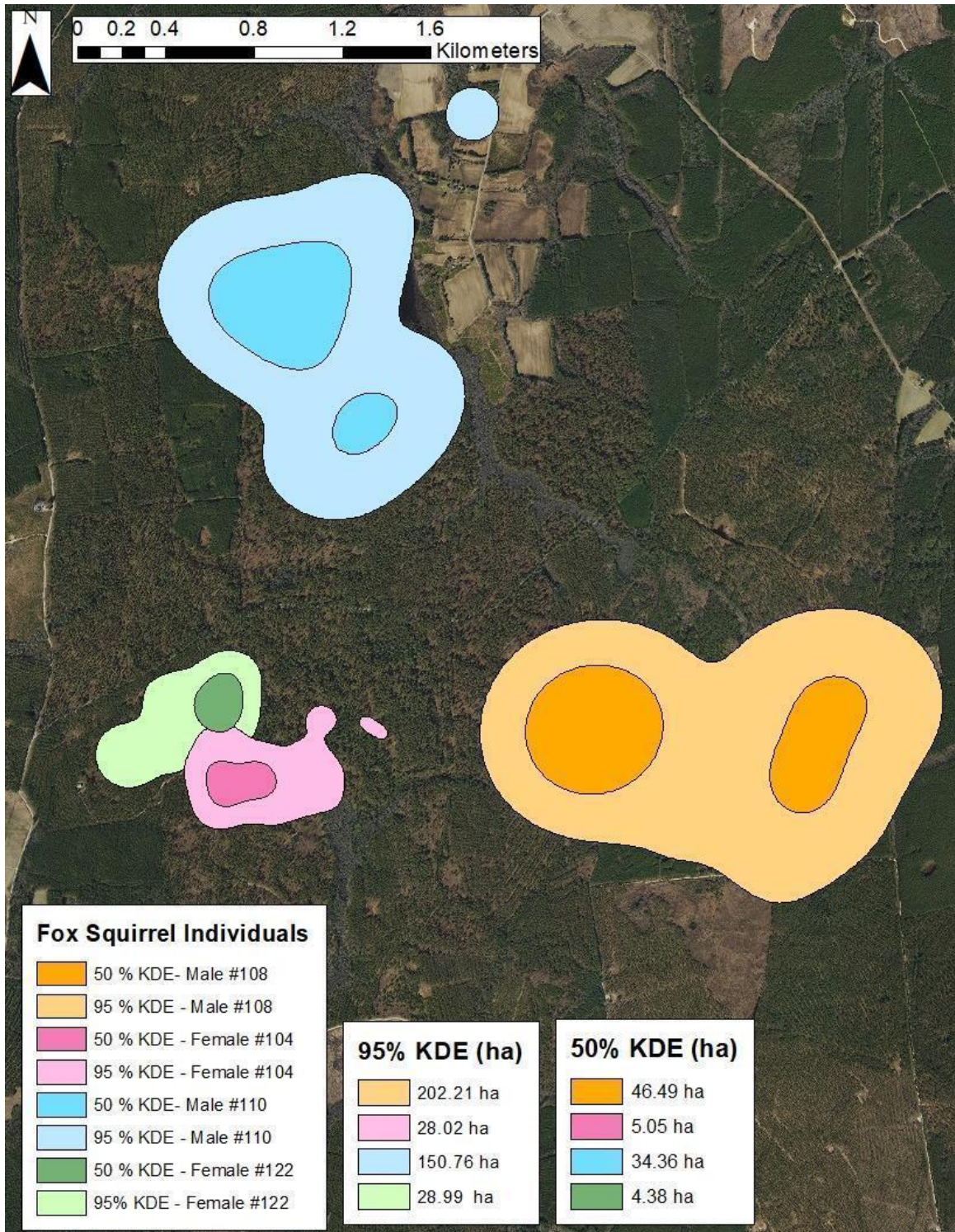


Figure 4. Second Order Habitat Selection. The relationship between southern fox squirrel probability of use of savanna and other cover types with the number of burns since 2019 at second order habitat selection on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2022.

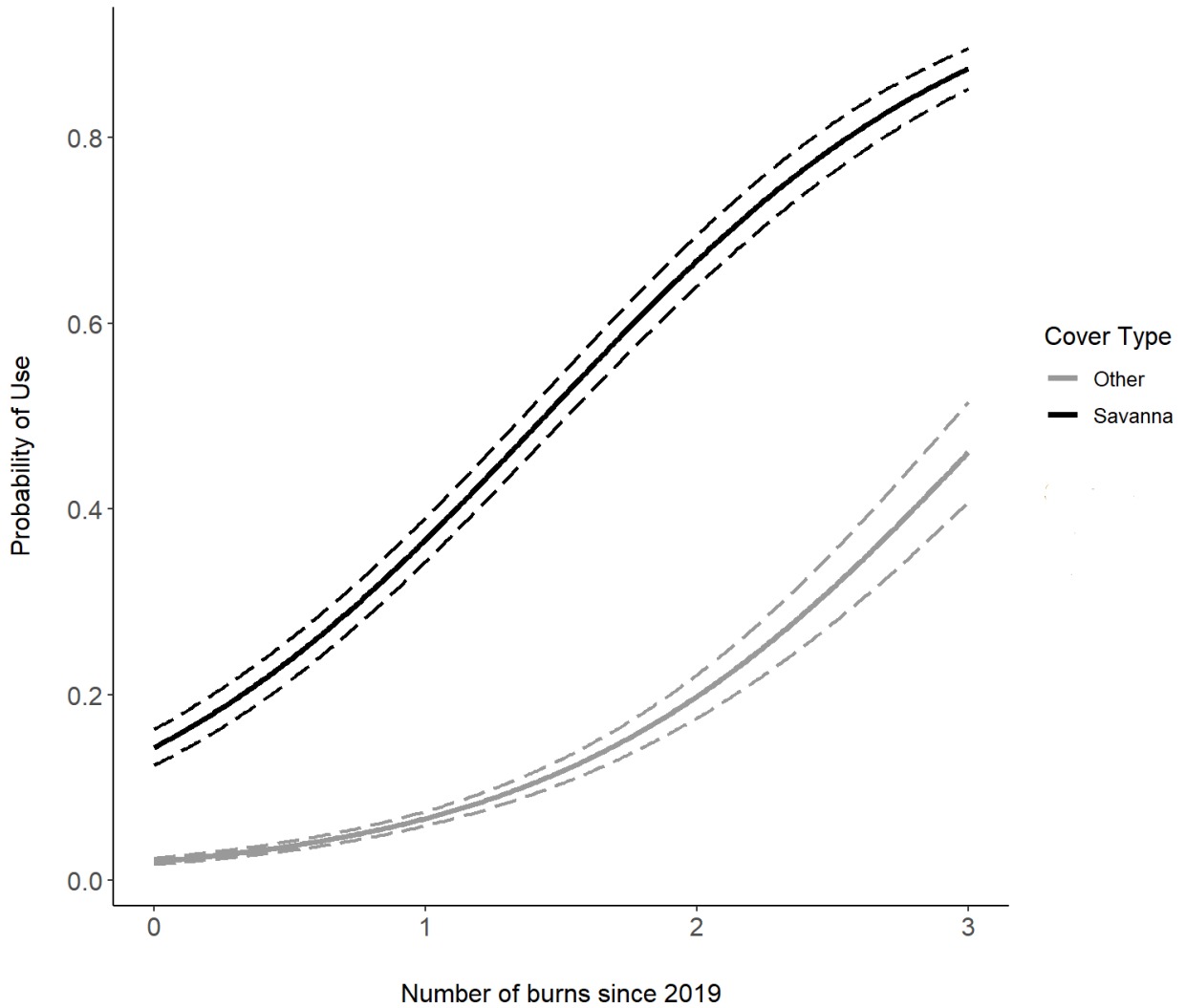
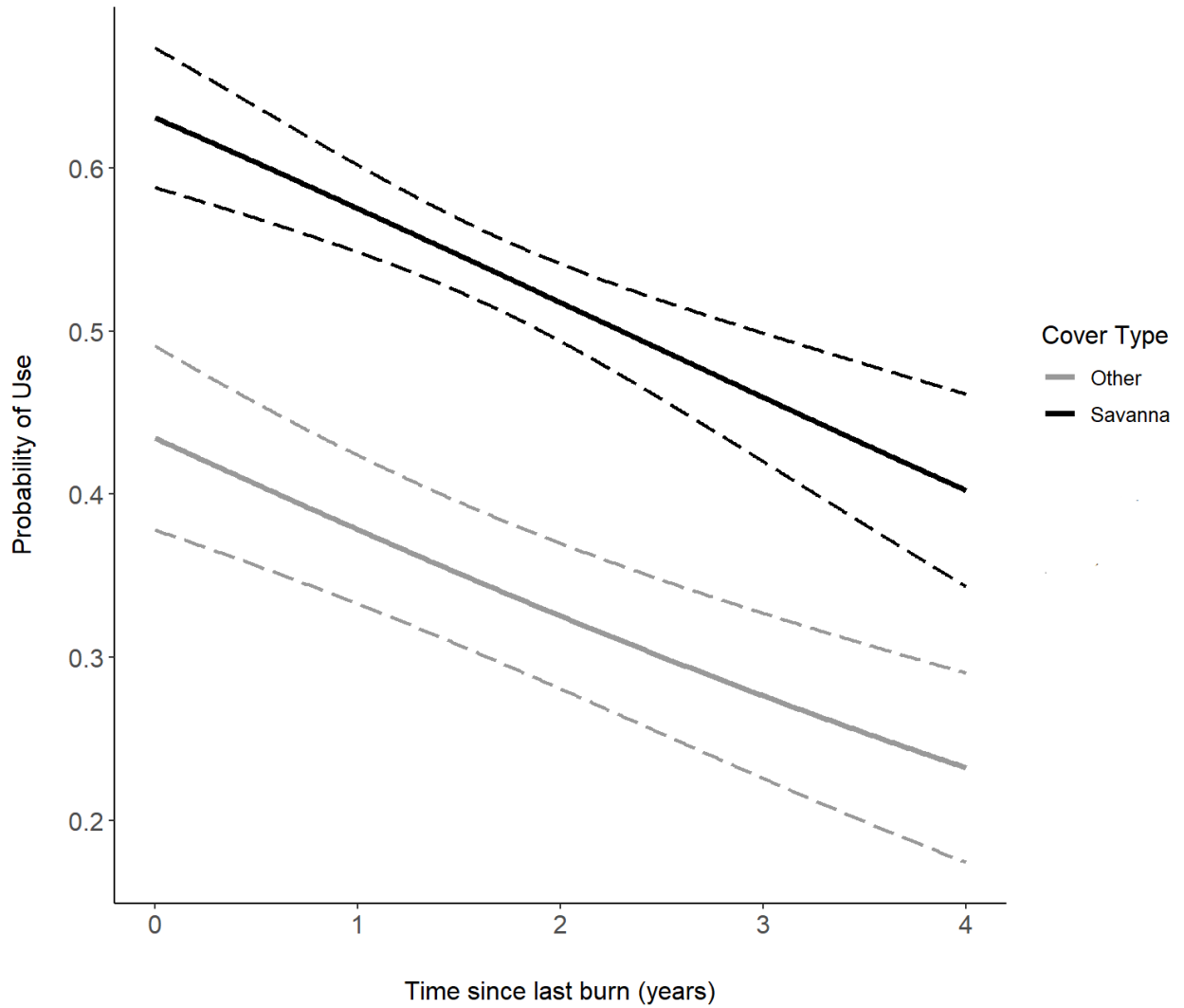


Figure 5. Third Order Habitat Selection. The relationship between southern fox squirrel probability of use of savanna and other cover types with the time since last burn (in years) at second order habitat selection on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2022.



Chapter 3. Southern Fox Squirrel (*Sciurus niger niger*) and Eastern Gray Squirrel (*Sciurus carolinensis*) interactions in a rare, fire-maintained ecosystem.

INTRODUCTION

Gray squirrels (*Sciurus carolinensis*) are sympatric in all areas of the southern fox squirrel (*S. niger niger*) range in the southeastern U.S. (Edwards et al. 2003, McRobie et al. 2019). Historically, gray squirrels and southern fox squirrels co-existed in the same general areas despite having overlapping habitat needs for ecological traits such as foraging and nesting (Edwards et al. 2003). Specifically, both species utilize hard and soft mast from different hardwood species such as oak (*Quercus* spp.), black walnut (*Juglans nigra*), hickory (*Carya* spp.), pine (*Pinus* spp.), and American beech (*Fagus grandifolia*; Koprowski 1994a, Koprowski 1995b, Edwards et al. 2003, Wilson et al. 2020, Moncrief et al. 2012). Both squirrel species also use mature hardwood trees for drey nests or cavities as denning substrate (Koprowski 1994a, Koprowski 1995b, Edwards et al. 2003, and Moncrief et al. 2012).

Even with these overlapping ranges and similar resource selections, gray squirrels and southern fox squirrels use slightly different local niche spaces that helps minimize interspecific competition for limiting resources. Gray squirrels largely occupy deciduous forests (Steele and Koprowski 2011, Parker and Nilon 2008, Benson 2013, Sovie et al. 2021), whereas Southern fox squirrels are more likely to occupy open pine savanna woodlands and pine-hardwood mixed forests (Steele and Koprowski 2011, Sovie et al. 2021). Still, even with somewhat differentiated habitat niches, there are still areas of overlap and perceived competition, particularly in hardwood areas (Sovie et al. 2020, Sovie et al. 2021).

The Coastal Plain of the southeastern U.S. has gone through major habitat changes due to landscape conversions to agricultural or plantation forestry (Weigl et al. 1989, Edwards et al. 2003, Edwards and Laerm 2007). Where forests remain, natural disturbance regimes (i.e., frequent growing-season fire) have been replaced by fire suppression or at best, infrequent dormant season burning. Lack of prescribed or natural burning has shifted forest structure and composition towards conditions that favor gray squirrels (Whitaker and Hamilton 1998, Sovie et al. 2020, Sovie et al. 2021). Furthermore, fire suppression and forest mesophication have likely increased competition between southern fox squirrels and gray squirrels for remaining suitable habitats, as southern fox squirrels have a smaller usable niche space compared to gray squirrels (Sovie et al. 2020, Sovie et al. 2021).

The objectives of my study were to use two-species, single-season models to assess the effect of forest condition (e.g., basal area, canopy height), prescribed burn treatment (i.e., number of burns or fire frequency, time since last burn), and cover type classifications on occupancy estimates of southern fox squirrels given selection and potential competition with gray squirrels. I also aimed to estimate camera trapping level-of-effort (LOE) for southern fox squirrels in southeastern Virginia using a single-species occupancy model assessing time since last burn (years) informed by two-species occupancy modeling. Further, I aimed to analyze environmental variables including Julian Day, and weather/thermal conditions to assess if that would affect southern fox squirrel detection probabilities. I predicted that probable southern fox squirrel occupancy would be highest in recently burned areas of pine-hardwood mixed savanna in the absence of gray squirrels. Further, we predicted that fox squirrel detection would be

negatively influenced by greater amounts of daily precipitation and extreme daily temperatures (high heat or freezing temperatures).

METHODS

Camera Surveys

I deployed trail cameras (Bushnell Trophy HD cameras, Bushnell Outdoor Products, Overland, KS) at FB and BWPGC to initially assess the presence of southern fox squirrels and gray squirrels following the methods of Tye et al. (2015) and Greene and McCleery (2017). Sampling consisted of independent transects consisting of five cameras each. Site selection was based on stratified, random points in ArcMap 10.8 (ERSI Inc., Redlands, CA) from a point grid generated off of the boundary coordinates of the study sites. I stratified points using land cover as delineated by the National Land Cover Database, 2019 release (Dewitz and USGS, 2022). Prior to final selection, I confirmed the presence of desired cover types through visual inspection against U.S. Department of Agriculture NAIP aerial imagery, (2015, USDAFSA-APFO Aerial Photography Field Office, Salt Lake City, UT) where points within undesirable cover types such as open water and buildings, were avoided. I considered desired cover types as those that had a high probability of squirrel detection, including interior pine/hardwood forests, hardwood bottomland forests, pine woodlands, and pine/hardwood savannas. Finally, I randomly selected nine transect sites based on presence of suspected preferred southern fox squirrel habitat to maximize detection probability.

Fox squirrels have been previously identified at BWPGC (B. Clontz, The Nature Conservancy, personal communication, 3/1/2018) whereas gray squirrels are known to be

present on both study sites. Camera-trapping efforts at BWPGC were focused on the main broad cover types on the study site: mature upland loblolly pine savannas, loblolly pine/hardwood forests, and bottomland hardwood-dominant riparian areas. At FB, we deployed camera transects in mature upland hardwood forests, upland loblolly pine/hardwood forests, upland loblolly pine forests, and bottomland hardwood forests as we thought these sites were most likely to be used by either the southern fox squirrel and/or the eastern fox squirrel (*S. n. vulpinus*) which occurs in the Midwest of the U.S. through central Virginia to the west of BWPGC, if present. Here, I aimed to differentiate Sciurid species based primarily on pelage and size (Edwards et al. 2003, Tye et al. 2015, SCDNR 2020).

I deployed cameras from October 2019 to October 2020 on both BWPGC and FB. Due to equipment restraints, I deployed only three random transects of 5 cameras each for approximately 28 consecutive days. At the end of each 28-day rotation, I moved all cameras to another grouping of three randomly chosen transect sites. I used three different rotations around the landscape for a total of nine randomly chosen transect locations. At each transect, I established five cameras consecutively at 250 m intervals to ensure independence of sample locations, as well as independence between camera survey transects (Tye et al. 2015), thereby maximizing the probability of determining occupancy among cover types of interest (Greene and McCleery 2017). Therefore, each transect was 1,000 m in length.

At each survey location, I placed a camera on the nearest tree to the assigned point 50–70 cm above the ground and pointed them at bait stations consisting of a nut and berry suet mixture (Greene and McCleery 2017). I used suet cakes as bait to increase

capture potential (Curtis and Sullivan 2001, Edwards et al. 2003), placing bait stations no more than 10 m from the camera and 30–70 cm from the ground attached to a tree (Boone et al. 2017).

I then used DeerLab (2013, DeerLab, Inc. Jacksonville, FL) to identify all observed mammals to species. I assessed the presence/absence of southern fox squirrels and eastern gray squirrels using occupancy analysis for both field sites. Presence or absence was represented in the database by a binary “1” or “0” value. The sample interval reflected time between camera deployments (i.e., 28 days) and a duration of 1-year (from October 2019 to October 2020). To standardize occurrence data, I also identified the total camera trap days and trap success of both fox and gray squirrels. I defined a “trap day” as a full 24-hour period in which a single camera was deployed. In calculating trap success, I considered an event to be the one instance where an individual animal entered the camera frame. From there, I standardized the events by calculating those frequencies per 100 trap days with the formula: $\frac{n}{t} = \frac{x}{100}$ where n is the frequency of events identified from a single species and t is the number of trap days for the survey period.

Predictor Variables

I considered six different covariates for two-species occupancy (ψ) combinations of a forest cover model (Canopy Cover + Basal Area) as well as Canopy Cover and Basal Area separately, two fire frequency models (Number of burns since 2019, Time since last burn), canopy height model, and general cover type model (savanna; Table 6). I considered these variables as they would be directly related to forest stratification and vegetation structure useful for further predictive efforts across the larger landscape (Hayes et al. 1981, Deuser 1988). Basal area and canopy closure were collected in the

field with a 10 basal area factor prism and concave spherical densitometer (Lemmon 1957), whereas average canopy height was calculated originating from USGS 2014 LiDAR point clouds (VGIN 2016). I then used the package lidR (Roussel et al. 2020) in R to create a canopy height model. I then used a 50 m circular moving window analysis to find the focal mean of percent herbaceous height for all pixels across the landscape. The presence of savanna habitat (1 as savanna; 0 as other cover types) was considered as a covariate as BWPGC is mainly covered by loblolly pine woodland savannas. I reclassified landcover to savanna or not savanna by creating a supervised classification ensemble model from known areas of savanna on the landscape using a vegetation height layer (heights > 18 m; LANDFIRE 2022) and percent evergreen forest derived from the National Land Cover Database, 2019 release (> 90% evergreen cover type; Dewitz and USGS, 2022). I then cut predictions based on a threshold that maximized sensitivity and specificity in relation to the training point classifications.

Data Analysis

All data analysis was performed in R version 4.2.2 (R Core Team, 2022). To account for collinearity among our covariates, I used the package usdm (Naimi 2017) where any variables that tested above 0.7 in correlation were compared and the covariate with the least support was not included in our final model analysis (Ampacher et al. 2019). I standardized all continuous variables by scaling them using the scale function from the base package in R (MacKenzie et al. 2006, Fiske and Chandler 2011) and created dummy variables for categorical variables prior to analysis. I used single-season, two-species occupancy to specifically assess the selection and possible competition of southern fox squirrels and gray squirrels. I then modeled survey effort using single-

species occupancy and detection models informed by significant occupancy variables derived from two-species top modeling results.

Two-species Occupancy Modeling

I used the *wiqid* package in R (Meredith 2022) to assess interactions of gray squirrels and fox squirrels utilizing single-season, two-species occupancy modeling. Two-species occupancy models estimate the probability of a subordinate species at a site, conditional on the presence or absence of a dominant species. As our focus was on southern fox squirrel occupancy, and because gray squirrels have been documented to outcompete fox squirrels in closed canopy hardwood stands (Sovie et al 2020, Sovie et al. 2021), I considered gray squirrels to be dominant and fox squirrels to be the subordinate species. Gray squirrels are also known to be more aggressive with other species that overlap with their ranges (Wauters and Gurnell 2002, Sovie et al. 2021).

I focused on parameterization that assessed 1) ψ_{Ba} : the probability of fox squirrel occupancy in absence of gray squirrels; 2) ψ_{BA} : the probability of fox squirrel occupancy in the presence of gray squirrels, and 3) ψ_A : the probability of gray squirrel occupancy. I concurrently assessed *a priori* models regarding the interactions of gray squirrels and southern fox squirrels when gray squirrels were absent ($\psi_A:\psi_{Ba}$), and the interactions of gray squirrels and southern fox squirrels when gray squirrels are present ($\psi_A:\psi_{BA}$) for a total of 16 model interactions. Using Akaike's Information Criteria for small sample sizes (AIC_c), I considered models within 2 AIC_c units of the top models to be competing models (Burnham and Anderson 2002, Sovie et al. 2020). Of the covariates in the top models, I considered covariates with 95% confidence intervals (CI) not

crossing zero to be significant predictors of occupancy (Shake et al. 2011, Bowling et al. 2014).

Single-species Modeling and Level of Effort (LOE) Estimation

I performed single-species modeling using the package *wiqid* in R (Meredith 2022) to test single-season, single-species occupancy (ψ) and detection (ρ) for southern fox squirrels. To further inform land managers of southern fox squirrel survey efforts, we used results from occupancy modeling regarding time since last burn (years) to form a level of estimation plot. I used the formula provided by Wintle et al. (2012), $n =$

$$\frac{\log\left(\frac{\alpha}{1-\alpha}\right) - \log\left(\frac{\psi}{1-\psi}\right)}{\log(1-\rho)}$$

where α is a desired confidence level, or range of theoretical probabilities, ψ is occupancy, and ρ is detection probability, to estimate the total number of sequential non-detections (n) required to determine probable absence of southern fox squirrels. Detection covariates utilized in single-species occupancy models were maximum daily temperature ($^{\circ}\text{C}$), daily precipitation (mm), and Julian day standardized by year. Maximum daily temperature and daily precipitation were included in models because previous research has shown that fox squirrel activity is negatively correlated with these variables (Amspacher et al. 2019). Weather data were retrieved from the National Oceanic and Atmospheric Administration (NOAA) National Weather Station (NWS) office located in Wakefield, Virginia. The inclusion of Julian day as a covariate can provide insight into differing activity periods of fox squirrels, as activity peaks at different times of the year due to nesting, foraging, and caching activities (Trani et al. 2007).

RESULTS

From October 2019 to October 2020, I recorded 370 trap days per camera site for a total effort of 16,650 trap days across 45 camera sites at both BWPGC and FB. Within our entire survey period, I identified fox squirrels at 13 (29%) of the 45 camera sites at BWPGC. Based on pelage and visual inspection derived from live captures from a concurrent radio-tracking study, all fox squirrels at BWPGC were the southern subspecies. Overall, trap success for southern fox squirrels was low, with approximately 0.45 captures per 100 camera trap days at BWPGC. Gray squirrels were identified at 17 (38%) of the 45 camera sites at BWPGC. The trap success of gray squirrels at BWPGC was 0.73 captures per 100 camera trap days. I identified presence of competitive exclusion for southern fox and gray squirrels as they overlapped at only 2 (4%) of the 45 camera sites at BWPGC. At Fort Barfoot, I identified gray squirrels at 41 (91%) of the 45 camera sites. The trap success of gray squirrels at Fort Barfoot was 10.08 captures per 100 camera trap days. I failed to detect either eastern or southern fox squirrels at FB over the study, therefore I limited occupancy and detection analyses for both species to BWPGC.

Two-species Occupancy Modeling

In assessing interactions among single-season, two-species occupancy modeling, I identified that the top model explaining the species interaction factor of fox squirrels and gray squirrels was the influence of time since the last burn ($\psi_A:\psi_{Ba}$; Table 7). Whereas gray squirrel occupancy probability (ψ_A) increased the longer time persisted between burns ($\psi_A \beta_{\text{time since last burn}} = 0.75$, $SE = 2.12$). Moreover, within the interaction parameter $\psi_A:\psi_{Ba}$, southern fox squirrel occupancy probability in the absence of observed gray

squirrels (ψ_{BA}) decreased the longer time persisted between burns ($\psi_{BA} \beta_{\text{time since last burn}} = -1.44, SE = 0.72$; Figure 6). The model within 3.44 ΔAIC_c units of the top model also included time since last burn for gray squirrel occupancy probability (ψ_A), but conversely, southern fox squirrel occupancy where gray squirrels are present (ψ_{BA}). This model also identifies that gray squirrel occupancy probability (ψ_A) increased the longer time persisted between burns, and in the presence of gray squirrels, southern fox squirrel occupancy probability (ψ_{BA}) decreased the longer time persisted between burns. However, the ψ_{BA} parameter was considered not significant as the CI crossed zero (Table 8).

Single-species Modeling and Level of Effort (LOE) Estimation

I utilized time since last burn (years) covariate from our top two-species occupancy model to inform LOE in surveying southern fox squirrels. For southern fox squirrels, the top model contained the temperature covariate, however that was deemed insignificant as the CI crossed zero (Arnold 2010). Therefore, the ‘null’ model for detection (constant p) was retained over other detection covariates looking at imperfect detection (Table 9). Our informed single-season occupancy model revealed that southern fox squirrel occupancy decreased with time since last burn (years; Table 10). Furthermore, I estimated that the necessary LOE for sequential non-detections of southern fox squirrels would be 42 days for one year since last burn, and seven days for two or more years since the last burn (Figure 7).

DISCUSSION

Our results documenting southern fox squirrel and gray squirrel occupancy interactions indicate that probable fox squirrel occupancy increases with intense

prescribed burn rotational periods, particularly in the absence of gray squirrels, which mirrors other previous findings in the southeast. (Parker and Nilon 2008, Steele and Koprowski 2011, Benson 2013, Sovie et al. 2021). Specifically, fire creates the open, woodland ecosystems that fox squirrels select (Weigl et al. 1989, Engstrom 1993). Frequently burned areas at BWPGC include pine savannas/woodlands, pine/hardwood forests, and the edges of bottomland hardwoods as these wetland areas act as fire lines for prescribed burning. Gray squirrels more often inhabit areas of closed canopy cover that are characterized by hardwood dominant areas and hardwood bottomlands (Gilliam and Platt 1999, Sovie et al. 2021). However, because our top two-species occupancy model indicates that southern fox squirrels are selecting frequently burned areas regardless of cover type in the absence of gray squirrels, it appears that the species at BWPGC is responding not only to resource requirements but also the potential competition with gray squirrels.

Although there are viable populations of southern fox squirrels at BWPGC, occupancy is low throughout much of the area. As southern fox squirrels utilize hardwoods all throughout their range (Edwards et al. 1989, Prince et al. 2016, Lee et al. 2009), our data suggests that southern fox squirrels are avoiding gray squirrels in that they reside in areas they are sympatric, but particularly when gray squirrels are absent. Therefore, gray squirrel competition could be an additional variable that needs to be considered when managing populations of southern fox squirrels. Increasing pine-hardwood forests and hardwood stringers within savanna/woodland areas that are frequently burned at high rotational periods could benefit fox squirrel populations at study sites like BWPGC. Our detection analysis of southern fox squirrels revealed that

neither Julian Day, average daily temperature, nor precipitation influenced detection probability. There have been competing studies that reported time-varying weather variables such as high temperatures during the summer season to have negatively affected squirrel activity and therefore detection (Weigl et al. 1989, Ditgen et al. 2017). To counteract any effects of environmental variables on detection probabilities, managers should utilize multi-day surveys to account for any variations (Pynne et al. 2020).

Competition can be a complex process among species and there are many mechanisms to explain competition such as interference competition, exploitative competition, or apparent competition. The findings of our interaction study among gray or southern fox squirrels point more relevantly towards interference competition as gray squirrels are more aggressive and tend to push fox squirrels from areas of use. Additionally, this might also be considered exploitative competition as integration of hardwood woodlands tended to be a limiting resource at BWPGC and therefore gray squirrels are utilizing most of the hardwood resources that southern fox squirrels need. However, it would take more in-depth documentation on the landscape to ascertain the exact mechanism of competition among gray and fox squirrels to be able to identify hyper specific management actions for competition.

Camera trapping efforts confirmed that, despite the presence of putative suitable habitat, southern fox squirrels at BWPGC occurred at low to moderate occupancy levels, and therefore likely reflective densities, similar to current observations across much of the Southeast (Weigl et al. 1989, Loeb and Moncrief 1993, Trani et al. 2007). Also, neither the southern nor eastern fox squirrel was observed at FB despite anecdotal accounts of presence. Because our camera-trapping sessions often exceeded necessary

LOE duration in most instances at each camera site at BWPGC and FB, I have high confidence that there are no established populations of fox squirrels of either subspecies at FB presently, though I note much of this large installation has yet to be surveyed.

LITERATURE CITED

- Allen, A. W., Y. K. Bernal, and R. J. Moulton. 1996. Pine plantations and wildlife in the southeastern United States: an assessment of impacts and opportunities. Information and Technology report 3. U.S. Department of Interior National Biological Service, Washington, D.C.
- Amspacher, k., B. Bauer, J. Waldron, E. Wiggers, and S. Welch. 2019. *Sciurus niger niger* (southern fox squirrel) density and diurnal patterns, occupancy, and detection of sympatric southern fox squirrels and *S. carolinensis* (eastern gray squirrel) on Spring Island, SC. *Southeastern Naturalist* 18(2):321-333.
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information Criterion. *The Journal of Wildlife Management* 74(6): 1175-1178.
- Barkalow Jr., F. S. and R. F. Soots Jr. 1965. An improved gray squirrel nest box for ecological and management studies. *The Journal of Wildlife Management* 29(4):679-684.
- Benson, E. 2013. The urbanization of the eastern gray squirrel in the United States. *Journal American History* 100(3): 691-710.
- Boone, W. W., R. A. McCleery, and B. E. Reichert. 2017. Fox squirrel response to forest restoration treatments in longleaf pine. *Journal of Mammalogy* 98(6):1594-1603.
- Bowling, S. A., C. E. Moorman, C. S. Deperno, and B. Gardner. 2014. Influence of landscape composition on northern bobwhite population response to field border establishment. *The Journal of Wildlife Management* 78(1):93-100.
- Bradshaw, D. S. and B. D. Watts. 2003. Investigation of red-cockaded woodpeckers in Virginia: year 2003. College of William and Mary, Center for Conservation Biology Technical Report Series CCBTR-03-10, Williamsburg, Virginia.
- Burnham, K. P. and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261-304.
- Burnham, K. P. and D. R. Anderson, editors. 2002. *Model selection and multimodel inference: a practical information-theoretic approach* (2nd Edition). Springer, New York, New York.
- Conner, L. M. 2000. Home range sizes of fox squirrels in Southwest Georgia. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:400-406.
- Conner, L. M., J. L. Landers, and W. K. Michener. 1999. Fox squirrel and gray squirrel associations within minimally disturbed longleaf pine forests. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 53:364-374.

- Curtis, P. A. and K. L. Sullivan. 2001. Tree squirrels: wildlife damage fact sheet. Cornell Cooperative Extension, Ithaca, New York.
- Diggins, C. A., L. M. Gilley, C. A. Kelly, and W. M. Ford. 2016. Comparison of survey techniques on detection of northern flying squirrels. *Wildlife Society Bulletin* 40(4):645-662.
- Deuser, R. D., J. Dooley, Jr. and G. J. Taylor. 1988. Habitat structure, forest composition and landscape dimensions as components of habitat suitability for the Delmarva fox squirrel. Pages 414-421 *in* Management of amphibians, reptiles, and small mammals in North America, R. C. Szaro, K. E. Severson, and D. R. Patton, editors. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Dewitz, J. and U.S. Geological Survey. 2021. National Land Cover Database (NLCD) 2019 (version 2.0). U.S. Geological Survey Data Release. <<https://www.sciencebase.gov/catalog/item/5f21cef582cef313ed940043>>. Accessed 16 May 2023.
- Dey, D. C. J. M. Kabrick, and C. J. Schweitzer. 2017. Silviculture to restore oak savannas and woodlands. *Journal of Forestry* 115(3): 202-211.
- Edwards, J. W., D. C. Guynn, and M. R. Lennartz. 1989. Habitat use by southern fox squirrels in coastal South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 42:337-345.
- Edwards, E. W., D. G. Heckel, and D. C. Guynn. 1998. Niche overlap in sympatric populations of fox and gray squirrels. *The Journal of Wildlife Management* 62(1):354-363.
- Edwards, J. W., W. M. Ford, and G. Guynn. 2003. Fox and Gray Squirrels. Pages 248-267 *in* Feldhamer, G.A., B.C. Thompson and J.A. Chapman, editors. *Wild mammals of North America: Biology, Management, and Conservation*. Johns Hopkins University Press, Baltimore, Maryland.
- Edwards, J. W. and J. Laerm. 2007. Eastern fox squirrel. Pages 410-416 *in* M. K. Trani-Griep, W.M. Ford, and B.R. Chapman, editors. *The Land Manager's Guide to Mammals of the South*. The Nature Conservancy, Durham, North Carolina.
- Emrick, Verl R, Matthew Fields, and Jessica Fitzpatrick. 2018. Removal, Propagation, and Transplantation of Michaux's Sumac (*Rhus michauxii*) Colonies from the Infantry Platoon Battle Course, Fort Pickett –Maneuver Training Center, 2018. Virginia Conservation Management Institute, College of Natural Resources and Environment, Virginia Polytechnic Institute and State University. VTCMI-Technical Report 05- 2018. Blacksburg, Virginia.

- Fiske, I. J., and R. B. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43(10):1-23.
- Fleming, G. P., K. D. Patterson, and K. Taverna. 2021. *The Natural Communities of Virginia: a Classification of Ecological Community Groups and Community Types*. Third approximation. Version 3.3. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia.
- Gray, E. M., T. E. Dennis, and A. M. Baker. 2017. Can remote infrared cameras be used to differentiate small, sympatric mammal species? A case study of the black-tailed dusky antechinus, *Antechus arktos* and co-occurring small mammals in southeast Queensland, Australia. *PLoS One* 12(8):1-19.
- Greene, D. U., R. A. McCleery, L. M. Wagner, and E. P. Garrison. 2016. A comparison of four survey methods for detecting fox squirrels in the southeastern United States. *Journal of Fish and Wildlife Management*. 7(1):99-106.
- Greene, D. U. and R. A. McCleery. 2017. Multi-scale responses of fox squirrels to land-use changes in Florida: utilization mimics historic pine savannas. *Forest Ecology and Management* 391:42-51.
- Hayes, R. L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. United States Department of Interior Fish and Wildlife Service Report FWS/OBS-81/47, Washington, D.C.
- Kalen, N. J., V. R. Emrick, R. M. Schneider, and M. J. St. Germain. 2014. Large and mesomammal camera survey of Fort Pickett, Virginia. Report 03- 2014 of Virginia Conservation Management Institute, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Koprowski, J. L. 1994a. *Sciurus niger*. *Mammalian Species*. 471: 1-9.
- Koprowski, J.L. 1994b. *Sciurus carolinensis*. *Mammalian Species*. 471:1-9.
- Lashley, M. A., M. V. Cove, M.C. Chitwood, G. Penido, B. Gardner, C. S. DePerno, and C. E. Moorman. 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Scientific Reports* 8(4173):1-11.
- Lee, J.C., D. A. Obsorn, and K. V. Miller. 2009. Habitat use by a dense population of southern fox squirrels. *Southeastern Naturalist* 8(1):157-166.
- Lemmon, P. E. 1957. A new instrument for measuring forest overstory density. *Journal of Forestry* 55:667-668.
- Loeb, S. C. and M. R. Lennartz. 1989. The fox squirrel (*Sciurus niger*) in Southeastern pine-hardwood forests. Pages 142-145 in T. A. Waldrop, editor. *Proceedings of Pine-Hardwood Mixtures. A Symposium on Management and Ecology of the Type*. Southeastern Forest Experiment Stat, Asheville, North Carolina.

- Loeb, S. C. and N. C. Moncreif. 1993. The Biology of Fox Squirrels (*Sciurus niger*) in the Southeast: a review. Pages 1-19 in N. D. Moncreif, J. W. Edwards and P. A. Tappe, editors. 33 Proceedings of the Second Symposium on Southeastern Fox Squirrels, *Sciurus niger*. Virginia Museum of Natural History, Martinsville, Virginia.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington, Massachusetts.
- McCalip, B., B. P. Oswald, K. R. Kidd, Y. Weng, and K. W. Farrish. 2019. Site factors influence on herbaceous understory diversity in east Texas *Pinus palustris* savannas. *International Journal of Biology* 11(1):1-9.
- McRobie, H.R., N.D. Moncreif, and N. I. Mundy. 2019. Multiple origins of melanism in two species of North American tree squirrel (*Sciurus niger*). *BMC Evolutionary Biology* 19(140): 1-14.
- Moncreif, N.D., J. B. Lack, J.E. Maldonado, K. L. Bryant, C. W. Edwards, and R. A. Van Den Bussche. 2012. General lack of phylogeographic structure in two sympatric, forest obligate squirrels (*Sciurus niger* and *S. carolinensis*). *Journal of Mammalogy* 93(5): 1247-1264.
- Naimi, B. 2017. Usdm: Uncertainty Analysis of Species Distribution Models. Version 1.1-18. <<https://cran.r-project.org/web/packages/usdm>>. Accessed 6 October 2022.
- Nixon, C. M. Harvera, S. P. and L. P. Hansen. 1984. Effects of nest boxes on fox squirrel demography, conditions and shelter use. *The American Midland Naturalist* 112(1):157-171.
- Nowacki, G. J. and M. D. Abrams. 2008. The demise of fire and “mesophication” for forests in the eastern United States. *BioScience* 58(2): 123-138.
- Ngumbang, J., M. Meredith, J. Bryer, J. Kruschke, B. Neelon, and M. Schaub. 2022. wqid: Quick and Dirty Estimates for Wildlife Populations. R package ver. 0.3.3. <<http://cran.r-project.org/web/packages/wqid/index.html>>. Accessed on 7 April 2023.
- O’Connel, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera Traps in Animal Ecology: Methods and Analyses. Pages in 15-17. A. F. O’Conner, J.D. Nichols, and K.U. Karanth, editors. Springer Tokyo, Dordrecht, Heidelberg, London, New York.
- Parker, T. S., and C. H. Nilon. 2008. Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems* 11:243-255.

- Picman, J. and L. M. Schriml. 1994. A camera study of temporal patterns of nest predation in different habitats. *The Wilson Bulletin* 106(3):456-465.
- Prince, A., M. C. Chitwood, M. A. Lashley, C. S. Deperno, and C. E. Moorman. 2016. Resource selection by southeastern fox squirrels in a fire-maintained forest system. *Journal of Mammalogy* 97(2):631-638.
- Prince, A., C. S. DePerno, B. Gardner, and C. E. Moorman. 2014. Survival and home-range size of southeastern fox squirrels in North Carolina. *Southeastern Naturalist* 13(3):456-462.
- Pynne, J.T., J.M. Stober, and A. J. Edelman. 2020. Eastern fox squirrel (*Sciurus niger*) occupancy in fragmented montane longleaf pine forests. *Southeastern Naturalist* 19(2): 402-417.
- R Core Team. 2002. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robbins, L. E. and R. L. Meyers. 1992. Seasonal effects of prescribed burning in Florida: a review. Tall Timbers Research Station, miscellaneous Publication 8, Tallahassee, Florida.
- Roussel, J. R., D. Auty, N. C. Coops, P. Tompalski, T. R. H. Goodbody. 2020. LidR: R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment* 251:112061.
- Rovero, F. and A. R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46(5): 1011-1017.
- Shake, S. C., C. E. Moorman, and M. R. Burchell II. 2011. Cropland edge, forest succession, and landscape affect shrubland bird nest predation. *The Journal of Wildlife Management* 75(40): 825-835.
- Shuttleworth, C. M. 2002. The use of nest boxes by the red squirrel (*Sciurus vulgaris*) in a coniferous habitat. *Mammal Review* 29(1):61-66.
- South Carolina Department of Natural Resource (SCDNR). 2020. Wildlife- Species: Southern Fox Squirrel (*Sciurus niger niger*). South Carolina Department of Natural Resources, Columbia, South Carolina.
- Sovie, A. R., D. U. Greene, and R. A. McCleery. 2020. Woody cover mediates fox and gray squirrel interactions. *Frontiers in Ecology and Evolution* 8(239):1-10.
- Sovie, A.R., L. M. Conner, J. S. Brown, and R. A. McCleery. 2021. Increasing woody cover facilitates competitive exclusion of a savanna specialist. *Biological Conservation* 255:1-8.
- Steele, M. A. and P. D. Weigl. 1992. Energetics and path use in the fox squirrel *Sciurus niger*: responses to variation in prey profitability and path density. *The American Midland Naturalist* 128(1):156-167.

- Steele, M.A. and J. L. Koprowski. 2001. North American Tree Squirrel. Washington, DC: Smithsonian Institution Press.
- Trani, M. K., W. M. Ford, and B. R. Chapman, editors. 2007. The land manager's guide to mammals of the South. The Nature Conservancy, Durham, North Carolina.
- Tye, C.A, D. U. Greene, W. M. Giuliano, and R. A. McCleery. 2015. Using camera-trap photographs to identify individual fox squirrels (*Sciurus niger*) in the southeastern United States. *Wildlife Society Bulletin* 39(3):645-650.
- U.S. Fish and Wildlife Service (USFWS). 2015. Statuary and Executive Order Reviews: Endangered and Threatened Wildlife and Plants: Removal of the Delmarva Peninsula Fox Squirrel from the List of Endangered and Threatened Wildlife. U.S. Fish and Wildlife Service Federal Register: 70700, Department of Interior, Arlington, Virginia.
- Virginia Department of Wildlife Resources (VADWR). 2015. Virginia's 2015 Wildlife Action Plan. Virginia Department of Wildlife Resources, Henrico, Virginia.
- Virginia Department of Wildlife Resource (VADWR). 2020. Special Status Faunal Species in Virginia. Virginia Department of Wildlife Resources, Henrico, Virginia.
- Virginia Geographic Information Network (VGIN). 2016. LiDAR Point Cloud data in Virginia. <vgin.vdem.virginia.gov/apps/virginia-lidar-downloads/explore>. Accessed 6 October 2022.
- Watts, B. D. and S. R. Harding. 2007. Virginia red-cockaded woodpecker conservation plan. Center of Conservation Biology Technical Report Series, CCBTR-07-07, College of William and Mary, Williamsburg, Virginia.
- Wauters, L. A., and J. Gurnell. 2002. The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. *Ethology* 105(2) 1053-1071.
- Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha, and T. L. Sharpe. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the Southeast. Tall Timbers Research Station Bulletin No. 24, Tallahassee, Florida.
- Wintle, B. A., T. V. Walshe, K. M. Parris, and M. A. McCarthy. 2012. Designing occupancy surveys and interpreting non-detection when observations are imperfect. *Biodiversity Research* 18:417-424.
- Whitaker, J. O. and W. J. Hamilton. 1998. Mammals of the Eastern United States. Cornell University Press, Ithaca, New York.

Table 6. Covariates for remote camera locations for Southern fox squirrel (*Sciurus niger niger*) and gray squirrel (*Sciurus carolinensis*) occupancy and detection on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020.

Covariate	Description	Objective of Covariate
Julian Day	Julian day is a unit of measurement that standardizes yearly measurement by exactly 365 days.	Inclusion of Julian day as a detection covariate can give insight into differing activity periods from fox squirrels and gray squirrels as activity peaks at different times of the year due to nesting, foraging and caching activities (Trani et al. 2007).
Max Daily Temperature	The highest temperature recorded for each day of sampling measured in °C	Maximum daily temperature was obtained from the National Oceanic and Atmospheric Administration (NOAA) Weather Station (NWS) office located in Wakefield, Virginia. Max. daily temperature was included as extreme temperatures have been known to affect the detection probability of fox and gray squirrels (Amspacher et al. 2019, Pynne et al. 2020).
Daily Precipitation	Total daily precipitation recorded for each day of sampling measured in mm.	Total daily precipitation was obtained from the National Oceanic and Atmospheric Administration (NOAA) Weather Station (NWS) office located in Wakefield, Virginia. High values of total daily precipitation could affect activity levels of fox and gray squirrels, and could therefore affect detection probability. (Amspacher et al. 2019, Pynne et al. 2020)
Forest Condition	Forest condition included Percent Canopy Closure (CC) and Basal Area (BA)	Percent canopy cover was derived from on-site measurements using a concave spherical densiometer (Lemmon, 1957). Our goal is to capture fine scale differences between hardwood dominant areas and pine dominant areas that might affect fox squirrel and gray squirrel site selection (Greene and McCleery 2017). Whereas Basal area was

Savanna	The presence of either gray squirrels or fox squirrels at each camera location.	calculated in the field with a 10 basal area factor prism. Basal area of each camera location was calculated to demonstrate surrounding forest structure density (Hayes et al. 1981, Sovie et al. 2021).
Canopy Height	Canopy height model included the average canopy height at a 50m radius around the camera point.	Average canopy height was calculated originating from USGS 2014 LiDAR points clouds (VGIN 2016). I then used the package lidR (Roussel et al. 2020) in R to create a canopy height model. Canopy height has been known to be positively correlated with fox squirrels (Conner and Godbois 2003).
Burn Frequency	Burn frequency models included either the time since the last burn (TSB) in years, or number of burns since the beginning of 2017 (NOB). Data was collected from land managers at BWPGC.	Time since last burn and number of burns is important as it has been deemed an important management tool for fox squirrel habitat in other parts of their range (Conner et al. 1999).

Table 7. Southern fox squirrel (*Sciurus niger niger*) occupancy (ψ) and detection (ρ) models on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Models considered as having strong empirical support at $\Delta\text{AICc} < 2.0$ from the top model.

Model	AICc	ΔAICc	Model Likelihood	Model Wt.
$\psi\text{A}:\psi\text{Ba}$ (Time since last burn)	964.63	0.00	1.000	0.777
$\psi\text{A}:\psi\text{BA}$ (Time since last burn)	968.07	3.44	0.179	0.139
$\psi\text{A}:\psi\text{Ba}$ (.)	971.56	6.93	0.031	0.024
$\psi\text{A}:\psi\text{Ba}$ (Forest Condition)	972.44	7.81	0.020	0.016
$\psi\text{A}:\psi\text{Ba}$ (Savanna + Canopy Height)	972.90	8.27	0.016	0.012
$\psi\text{A}:\psi\text{BA}$ (Forest Condition)	972.92	8.29	0.016	0.012
$\psi\text{A}:\psi\text{BA}$ (.)	973.75	9.12	0.010	0.008
$\psi\text{A}:\psi\text{Ba}$ (Forest Condition + Savanna)	973.98	9.35	0.009	0.007
$\psi\text{A}:\psi\text{BA}$ (Canopy Cover + Canopy Height)	974.48	9.85	0.007	0.006
$\psi\text{A}:\psi\text{BA}$ (Forest Condition + Savanna)	975.23	10.61	0.005	0.004
$\psi\text{A}:\psi\text{Ba}$ (Canopy Cover + Canopy Height)	975.59	10.96	0.004	0.003
$\psi\text{A}:\psi\text{Ba}$ (Canopy Height)	975.69	11.06	0.004	0.003
$\psi\text{A}:\psi\text{BA}$ (Savanna + Canopy Height)	976.12	11.49	0.003	0.002
$\psi\text{A}:\psi\text{BA}$ (Canopy Height)	976.21	11.58	0.003	0.002
$\psi\text{A}:\psi\text{Ba}$ (Basal Area + Canopy Height)	977.77	13.14	0.001	0.001
$\psi\text{A}:\psi\text{BA}$ (Basal Area + Canopy Height)	979.26	14.63	0.001	0.001

Table 8. Southern fox squirrel (*Sciurus niger niger*) two-species occupancy (ψ) model parameter estimates and beta (β) output with standard error (SE), and 95% confidence intervals (CI) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Derived from the relationship between Time Since Burn (in years), gray squirrel occupancy, and southern fox squirrel occupancy when gray squirrels are absent indicated from the top model output $\psi_A:\psi_{Ba}$ (Time Since Burn), $\rho(\cdot)$. Significant variables denoted by *.

Model/Parameter	AICc	β Coeff.	SE	LCI	UCI
$\psi_A:\psi_{Ba}$ (Time since last burn)	964.63				
ψ_A (Time since last burn)		0.75	0.35	0.056	1.443
ψ_{Ba} (Time since last burn)		-1.44	0.72	-2.852	-0.029
$\psi_A:\psi_{BA}$ (Time since last burn)	968.07				
ψ_A (Time since last burn)		0.75	0.35	0.057	1.446
ψ_{Ba} (Time since last burn)		-10.00	18.59	-46.443	26.443

Table 9. Southern fox squirrel (*Sciurus niger niger*) single-species occupancy (ψ) and detection (ρ) models on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Models considered as having strong empirical support at $\Delta AIC_c < 2.0$ from the top model. Significant variables denoted by *.

Model	AIC_c	ΔAIC_c	Model Likelihood	Model Wt.
ψ (Time since last burn)*, ρ (Temperature)	394.23	0.00	1.00	0.34
ψ (Time since last burn)*, ρ (.)	395.65	1.43	0.49	0.17
ψ (Time since last burn), ρ (Temperature + Julian Day)	396.18	1.96	0.38	0.13
ψ (Time since last burn), ρ (Julian Day)	396.26	2.04	0.36	0.12
ψ (Time since last burn), ρ (Temperature + Precipitation)	396.64	2.42	0.30	0.10
ψ (Time since last burn), ρ (Precipitation)	397.81	3.59	0.17	0.06
ψ (Time since last burn), ρ (Precipitation + Julian Day)	398.57	4.34	0.11	0.04
ψ (Time since last burn), ρ (Temperature + Precipitation + Julian Day)	398.72	4.50	0.11	0.04

Table 10. Southern fox squirrel (*Sciurus niger niger*) single-species occupancy (ψ) model parameter estimates and beta (β) output with standard error (SE), and 95% confidence intervals (CI) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Derived from the model output ψ (Time since last burn), $\rho(\cdot)$

Occupancy Model					
Variable	β Coeff.	SE	LCI	UCI	Relationship
Intercept	-1.48	0.55	-2.56	-0.41	-
Time since last burn*	-1.44	0.72	-2.85	-0.03	-
Detection Model					
Variable	EST	SE	LCI	UCI	Relationship
Intercept	-3.61	0.18	-3.96	-3.26	-

Figure 6. Effect of time since last burn (in years) for eastern gray squirrel (*Sciurus carolinensis*) occupancy (ψ_A), and for southern fox squirrel (*Sciurus niger niger*) occupancy when gray squirrels are absent (ψ_{Ba}) at remote camera locations on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020. Relationship between time since burn, gray squirrel occupancy, and southern fox squirrel occupancy when gray squirrels are absent indicated from the output $\psi_A:\psi_{Ba}$ (Time Since Burn), $\rho(\cdot)$.

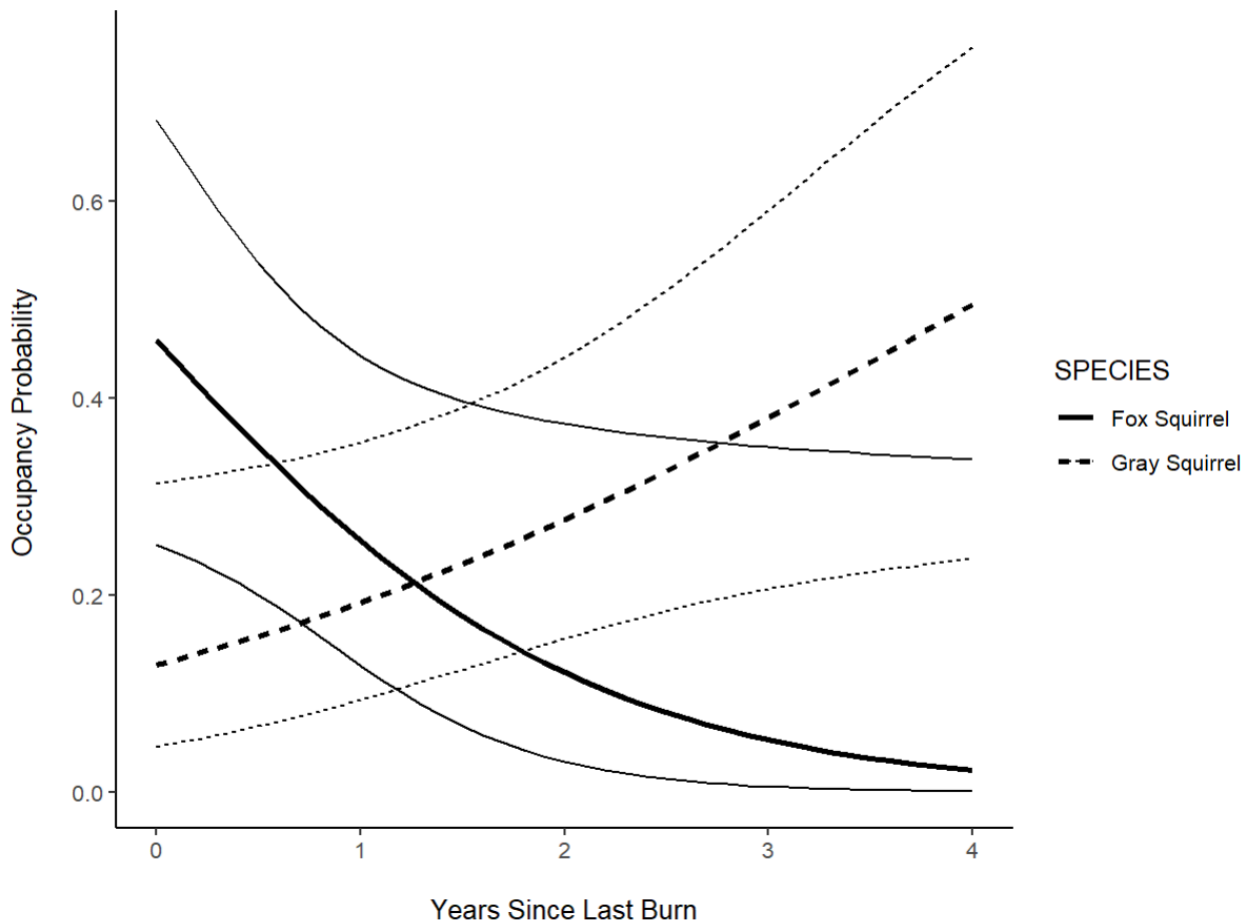
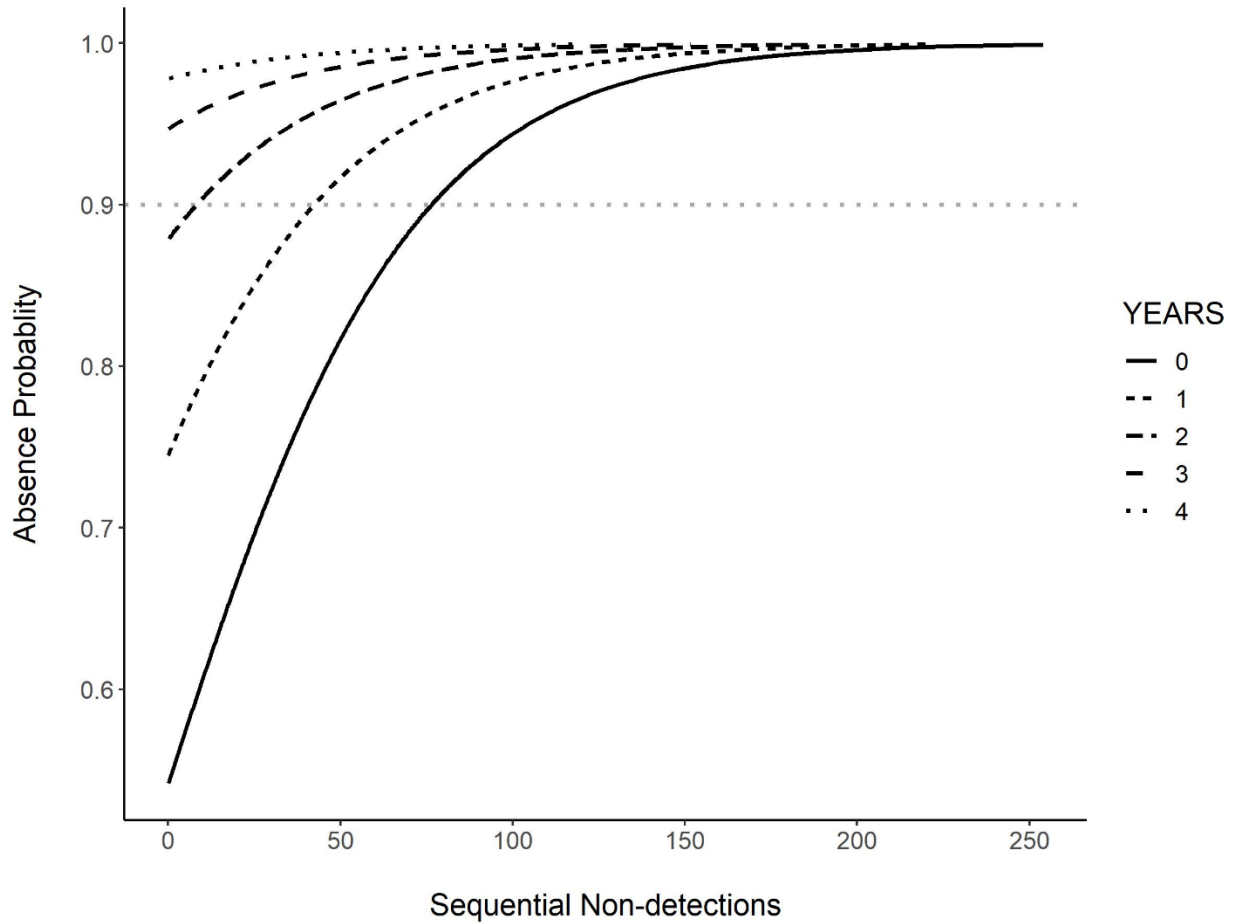


Figure 7. Detection Probability per camera rate per day of southern fox squirrels (*Sciurus niger niger*) based on time since last burn (years) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020.



CHAPTER 4: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Virginia Piedmont and Coastal Plain Associations

Though my work was limited in duration and geographic scope, it does not appear that either the southern fox squirrel or eastern fox squirrel currently occupies the lower Piedmont of Virginia in or around Fort Barfoot and suggests the region has not yet been colonized by eastern fox squirrels expanding east out of the Blue Ridge Mountains. Southern fox squirrels are present at BWPGC but at low numbers, as evidenced by the extensive survey effort required to confidently determine presence. Although suitable habitat at BWPGC occurs, much of the surrounding landscape is probably of marginal quality (i.e., intensive agriculture, pine plantations), hence populations at BWPGC may be somewhat isolated. Documenting presence of other extant populations of southern fox squirrels on the Coastal Plain of Virginia generally, and better defining the broader regional distribution specifically merits additional and more widespread surveys.

Future Habitat Management

For managers interested in documenting the presence of southern fox squirrels in the southeastern portion of Virginia, I suggest prioritizing initial camera surveys in mixed pine-hardwood or pine forests. Also, prescribed burn management was deemed the most important resource in the habitat it creates throughout my studies. Particularly, short-rotation, high intensity burning. As the savanna cover type was deemed important, areas of pine savannas should be maintained for southern fox squirrel habitat. However, integration of hardwoods are also deemed important for southern fox squirrels through other areas in their range. I also identified that southern fox squirrels may be trying to utilize hardwood-pine mixed areas and ecotones, but only in the absence of gray

squirrels. As gray squirrels have been found to utilize closed canopy areas and compete with southern fox squirrels in these instances, I suggest habitat management should follow high rotational (1-2 year) burns, keeping a fairly open canopy for pine savanna, mixed pine-hardwoods, and hardwood-pine ecotones throughout the southern fox squirrel range.

Appendix A, B, C, and D
Supplemental Tables, Figures, and Pictures

Appendix A

**Den site characteristics for southern fox squirrels (*Sciurus niger niger*)
at Big Woods Wildlife Management Area and Piney Grove Preservation,
Virginia, October 2022**

Table A.1 Individual tree characteristics of den and drey sites for radio collared southern fox squirrels (*Sciurus niger niger*) at Piney Grove Preservation, Sussex County, Virginia, 2022.

Squirrel ID*	Den #	Lat, Long	Den Type	Den Tree Species	Tree Height (m)	Den Height (m)
151.821	1	36.963829, -77.063603	Nest Box	Loblolly Pine (<i>Pinus taeda</i>)	23.82	3.8
151.821	2	36.965348, -77.065807	Drey	Loblolly Pine	29.2	25.6
151.821	3	36.964992, -77.05312	Drey	Loblolly Pine	18.28	12.19
151.821	4	36.96378, -77.058749	Drey	Loblolly Pine	19.4	14.6
151.821	5	36.96141, -77.062902	Nest Box	Loblolly Pine	27.96	4.11
151.320	6	36.979223, -77.075555	Nest Box	Loblolly Pine	24.46	3.53
151.320	7	36.977714, -77.076507	Drey	Loblolly Pine	28.09	18
151.320	8	36.983493, -77.079383	Drey	Loblolly Pine	14.14	12.4
151.320	9	36.983647, -77.080626	Drey	Loblolly Pine	18.53	15.71
151.280	10	36.96642, -77.08478	Drey	Loblolly Pine	20.78	17.5
151.280	11	36.965033, -77.08668	Drey	Loblolly Pine	16.87	14
151.280	12	36.96414, -77.08774	Drey	Loblolly Pine	26.65	24.5
151.280	13	36.964599, -77.085291	Nest Box	Loblolly Pine	13.72	3.5
151.760	14	36.963302, -77.085157	Nest Box	Loblolly Pine	27.66	4.13
151.760	15	36.964264, -77.084306	Nest Box	Loblolly Pine	25.45	3.58
151.760	16	36.963759, -77.085335	Nest Box	Loblolly Pine	27.86	3.73
151.760	17	36.962858, -77.084429	Nest Box	Loblolly Pine	26.12	3.6
151.760	18	36.963487, -77.084693	Drey	White Oak (<i>Quercus alba</i>)	28.28	21.78
151.760	19	36.9634, -77.08303	Drey	Loblolly Pine	27.08	24.88
151.760	20	36.96459, -77.084049	Drey	Loblolly Pine	27.2	25.36
151.760	21	36.962998, -77.083539	Drey	Loblolly Pine	26.18	21.33
151.760	22	36.96176, -77.08196	Natural Cavity	Loblolly Pine	25.62	14.56
*151.821, 151.320 = Male	*151.280, 151.760 = Female			$\bar{x} \pm SE:$	23.79 \pm 1.03	13.29 \pm 1.79

Figure A.1 Southern fox squirrel 95% KDE and den sites for individual females on Piney Grove Preservation, and Military Training Center Fort Barfoot, Virginia, 2022.

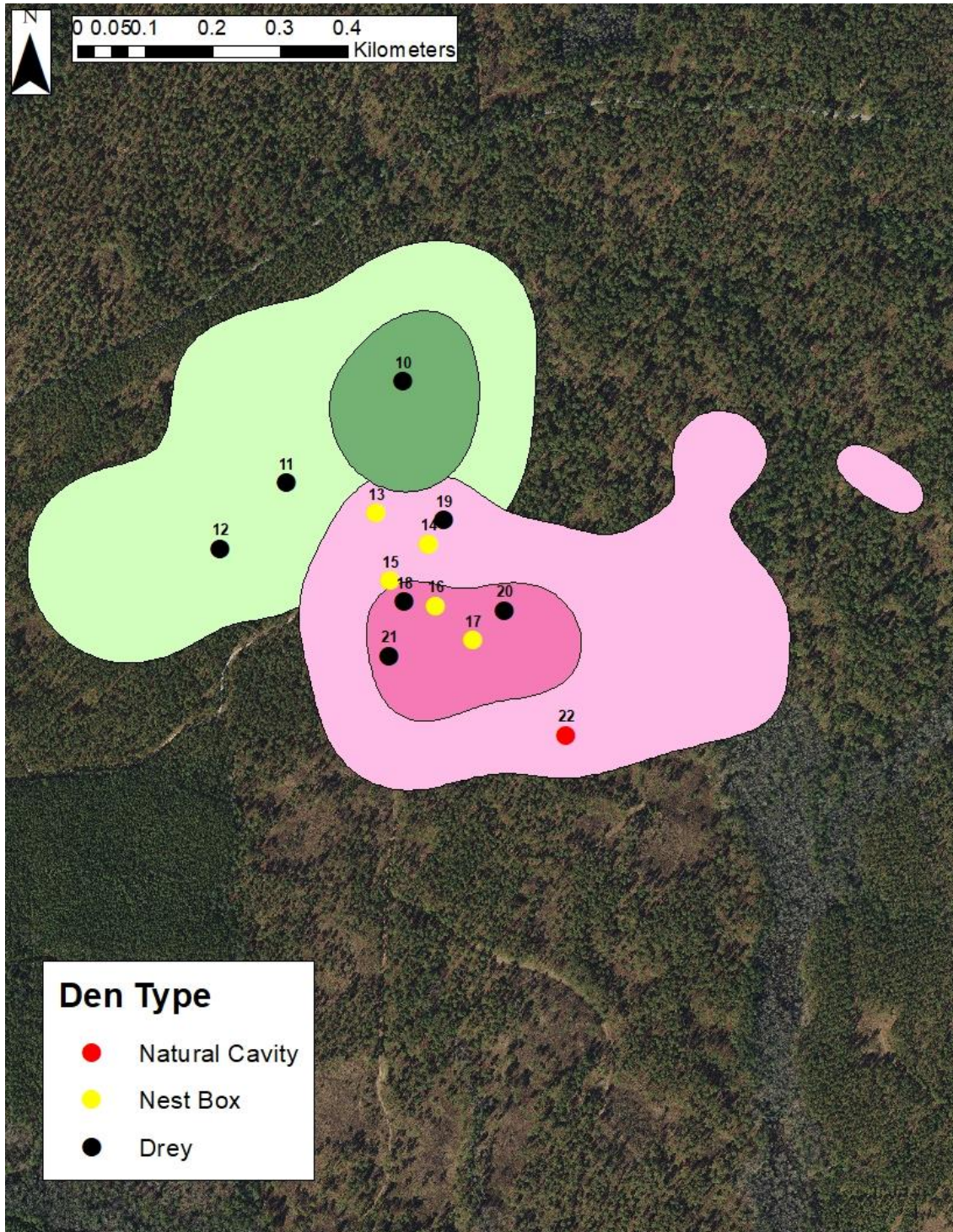
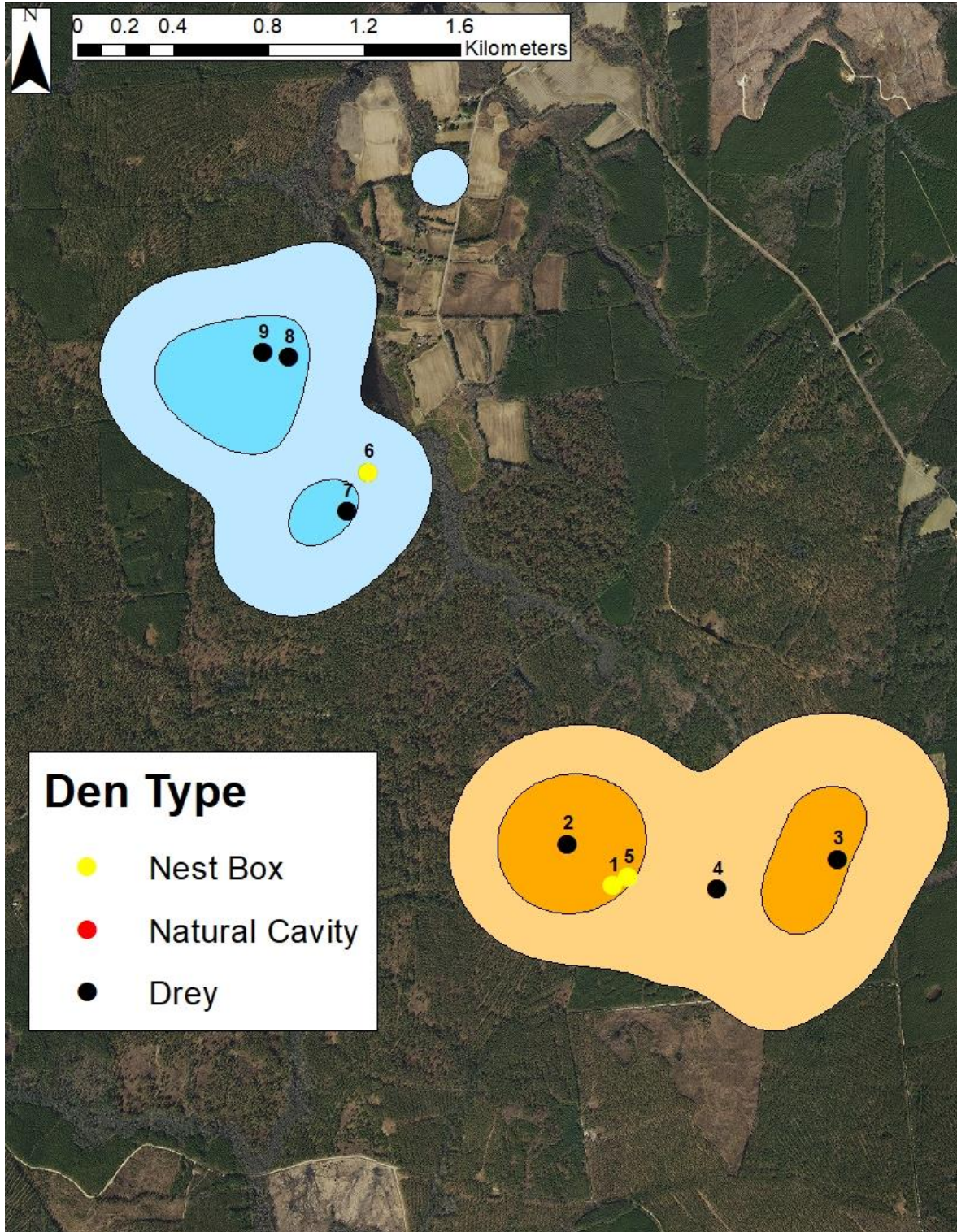


Figure A.2 Southern fox squirrel 95% KDE and den sites for individual males on Piney Grove Preservation, and Military Training Center Fort Barfoot, Virginia, 2022.



Appendix B

**Species distribution models of southern fox squirrels (*Sciurus niger niger*)
in the Coastal Plain Regions of Virginia, 2020-2022.**

Species distribution models of the southern fox squirrel in the Coastal Plain of Virginia

It is important to identify the spatial ecology and distribution of a species in order to properly manage it, especially for examples such as the southern fox squirrel in Virginia with rare and sparse populations. Documentation can reveal important habitat requirements and ecological specialization. It can also yield to bioindications of the surrounding landscape and act as a base map for management (Greene and McCleery 2017, Hernandez et al. 2006).

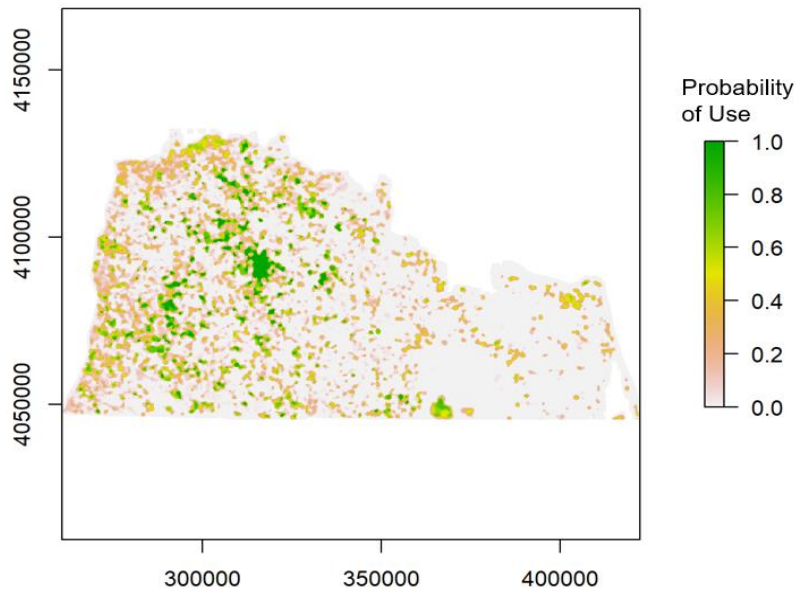
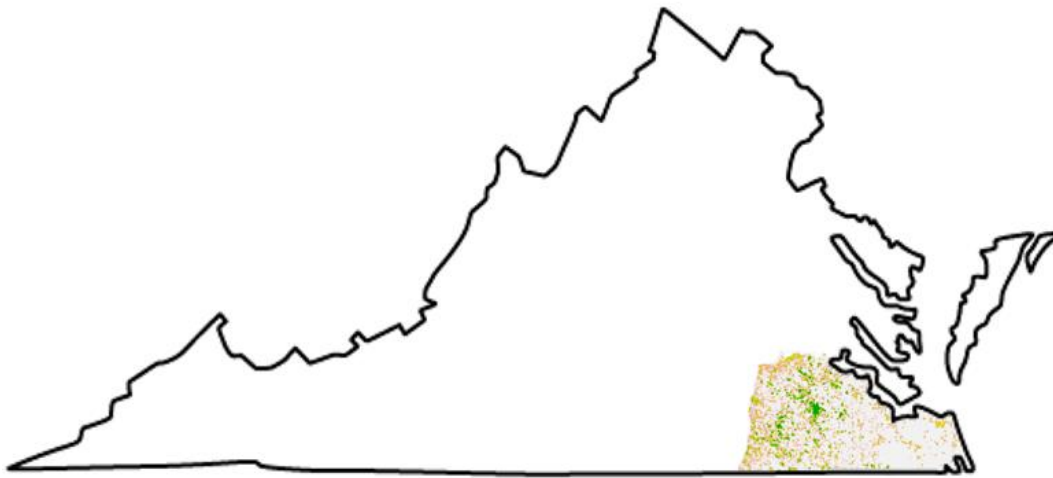
By utilizing species distribution models, I sought to predict the distribution of southern fox squirrels in the Southern Coastal Plain region in Virginia to aid in future management. I first included all locations derived from our occupancy and live trapping studies as well as any other opportunistic observations from land managers, and the general public. Variables I included were cover types from the 2019 National Land Cover database, 2019 release (Dewitz and USGS 2022), canopy cover, tree height, aspect, elevation, slope, and fuel disturbance looking at fire and mechanical management history from LANDFIRE (LANDFIRE 2014, LANDFIRE 2020a, LANDFIRE 2020b, LANDFIRE 2020c, LANDFIRE 2022a, LANDFIRE 2022b, LANDFIRE 2022c), forest fragmentation created in ArcGIS (UCONN CLEAR 2023), as well as mean annual temperature, and mean annual precipitation from PRISM (PRISM, 2023). With each variable, I created a circular moving window analysis to find the focal mean for each point at a 700m buffer.

Prior to analysis I tested variable importance and correlation using `vifcor` with the `usdm` package in R (Naimi 2017). I then used package `sdm` in R (Naimi and Aruajo 2021) to test species distribution probabilities based on the chosen variables. Following Jepson et al. (2011), I used the average area under the curve (AUC) across 50 model replicates in bootstrap form to assess model performance as mean AUC values decrease bias and stabilize results (De La Cruz and Ward 2016). AUC values above 0.5 and closest to 1 reflect suitable habitat conditions and increased model efficiency (De La Cruz and Ward 2016, Swets 1988).

Variable importance and model performance reflected selection of the following variables for the distribution model: mean elevation, small forest fragmentation, forest edges, deciduous, mixed, evergreen, and cultivated crop cover

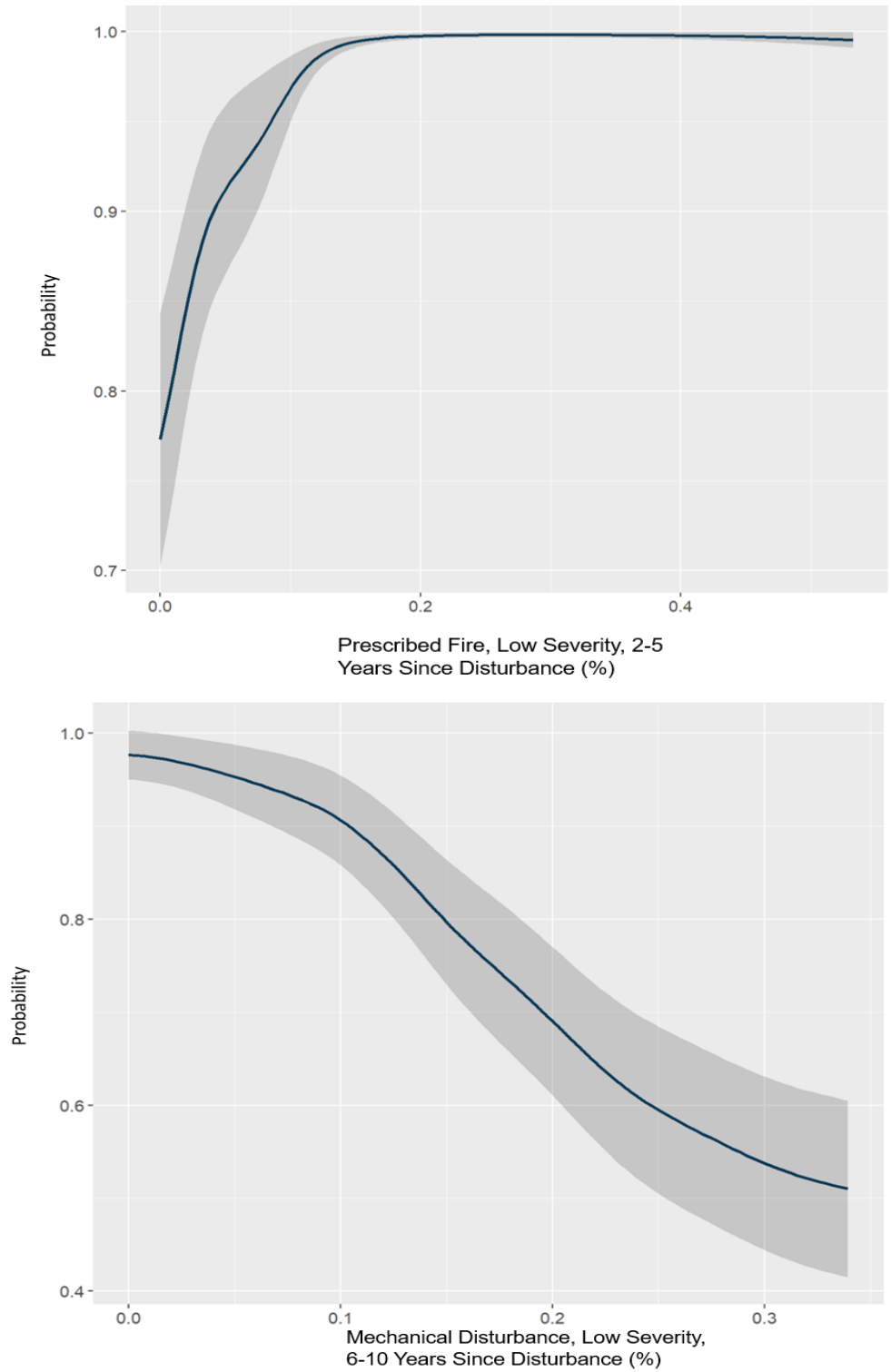
types, and prescribed burn disturbance (Figure B.2, Appendix B). Using a GLM in R, I predicted the presence probabilities of southern fox squirrels across the landscape based on the variables deemed important above (Figure B.1, Appendix B). Our results reflected southern fox squirrel selection for low severity, 2-5 year rotational burns as well as selection for the evergreen cover type. Selection also included minimal amounts of deciduous cover types, but generally decreased with increasing percentages of deciduous forest cover types, mixed forest cover types, and cultivated crop cover types. Elevation at about 30 m had the highest southern fox squirrel probability of use, however, that also generally aligns with the southeastern region of Virginia. Otherwise, southern fox squirrel probabilities generally decreased with increasing areas of mechanical disturbances, small core forests, and forest edges.

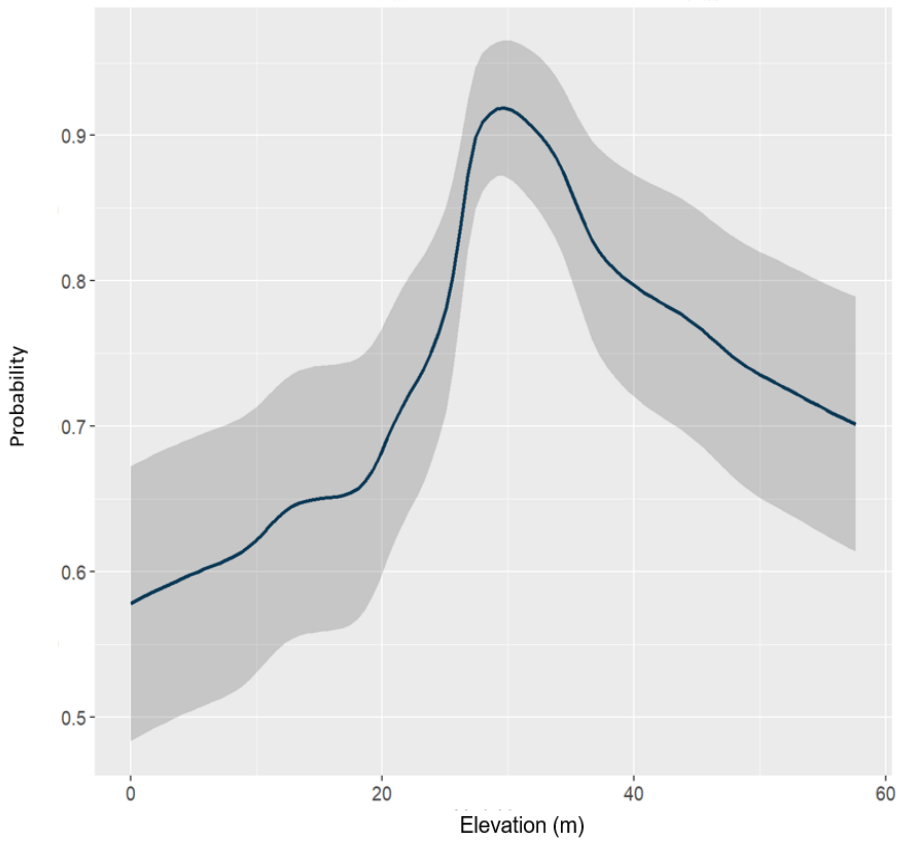
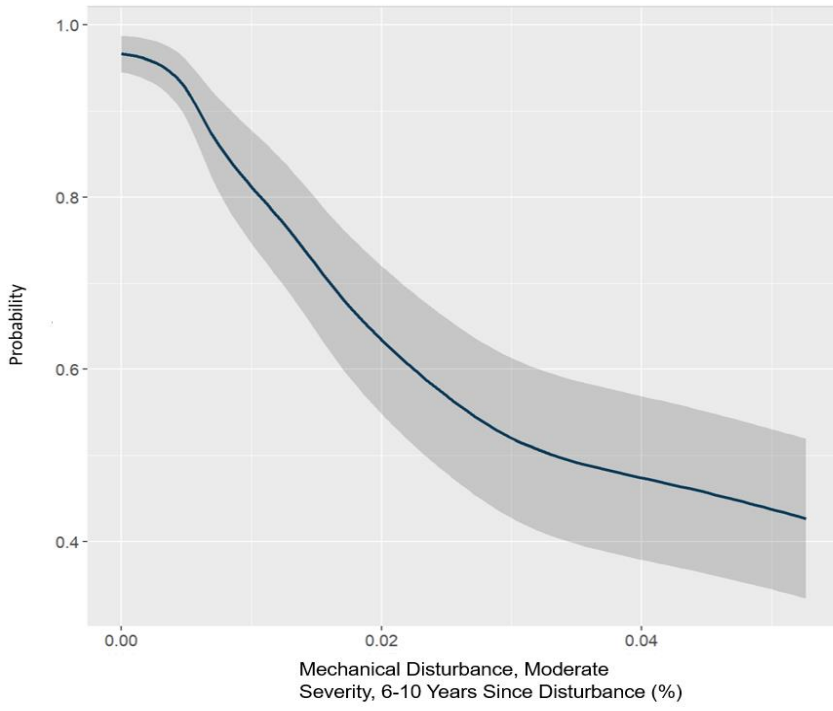
Figure B.1 Species Distribution Model (SDM) predictive map for identified southern fox squirrel (*Sciurus niger niger*) locations in the Southern Coastal Plain Region of Virginia

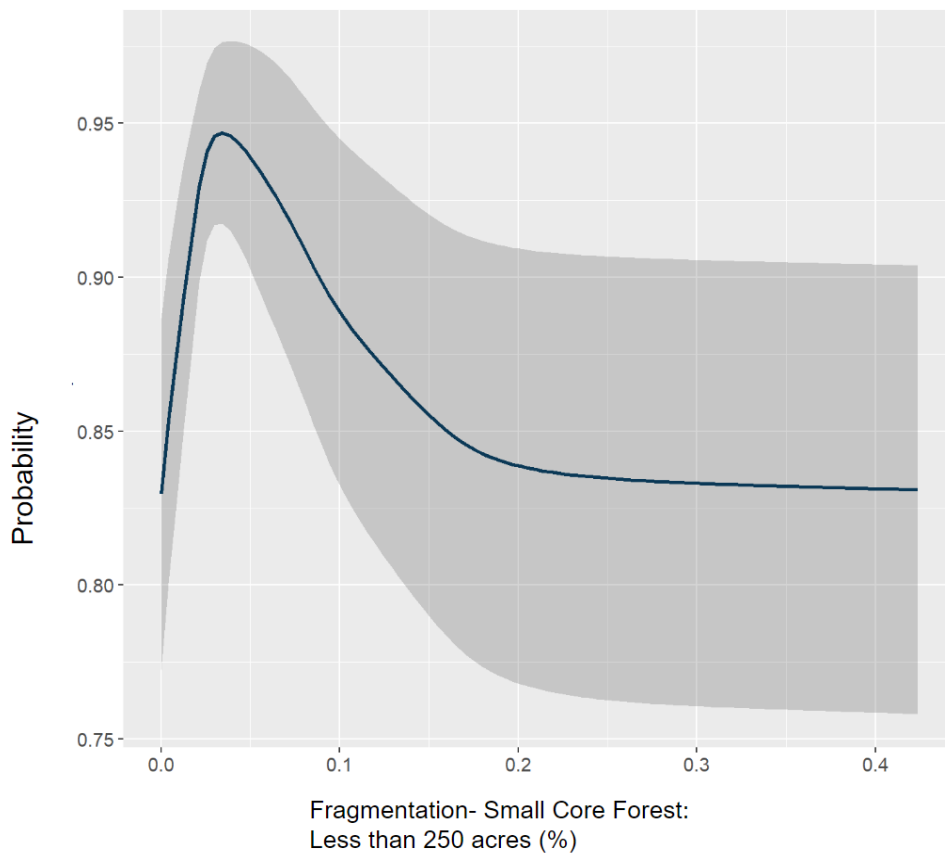
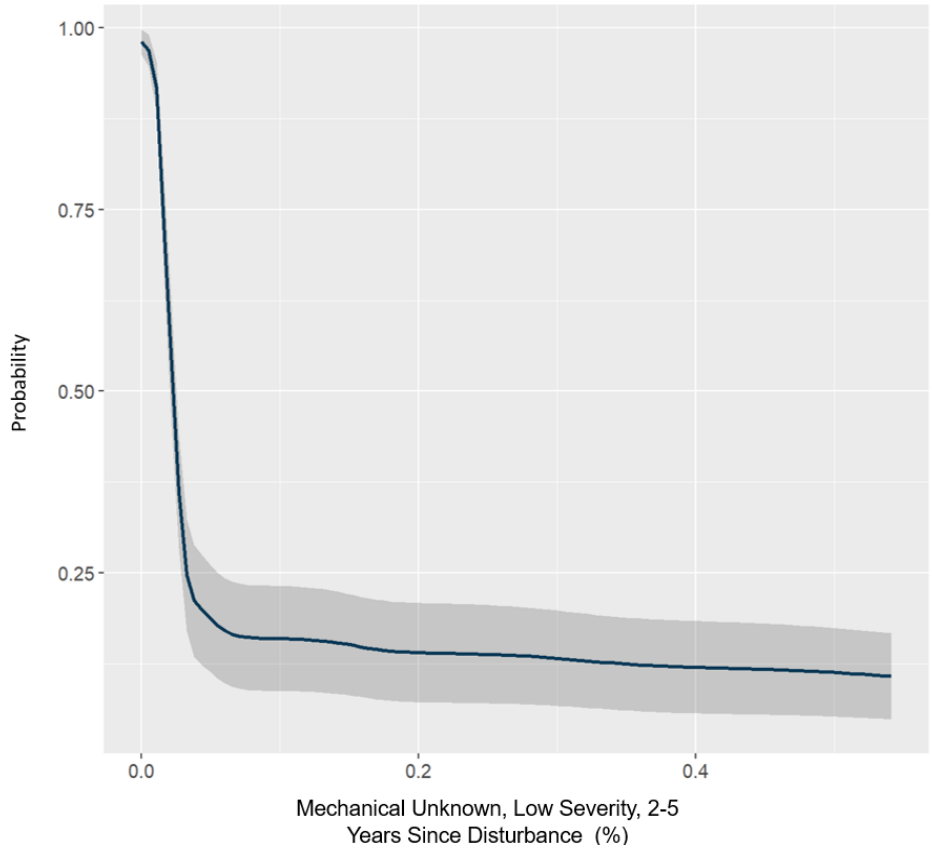


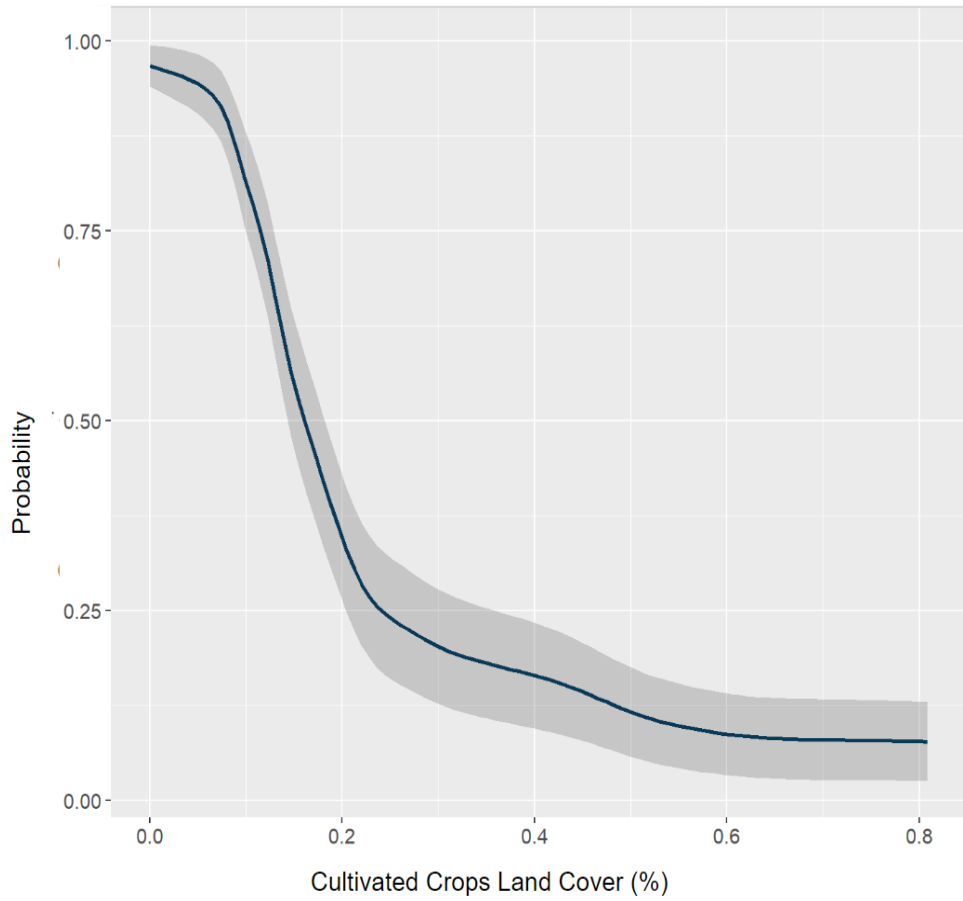
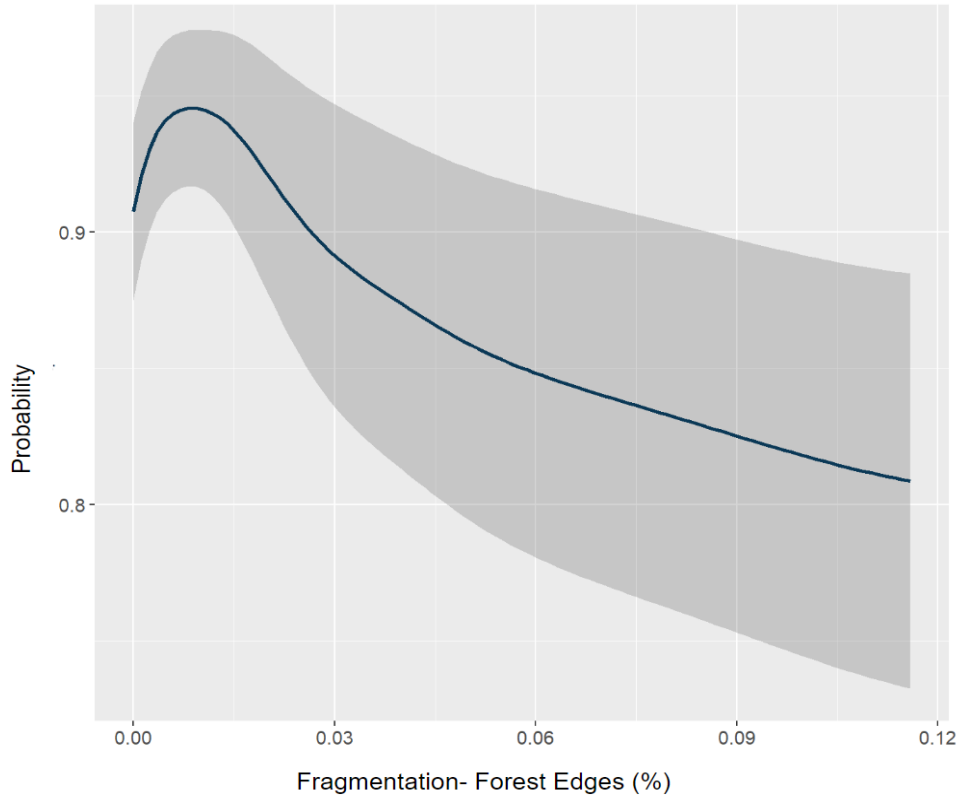
Method	AUC	COR	TSS	Deviance
GLM	0.98	0.92	0.96	1.64

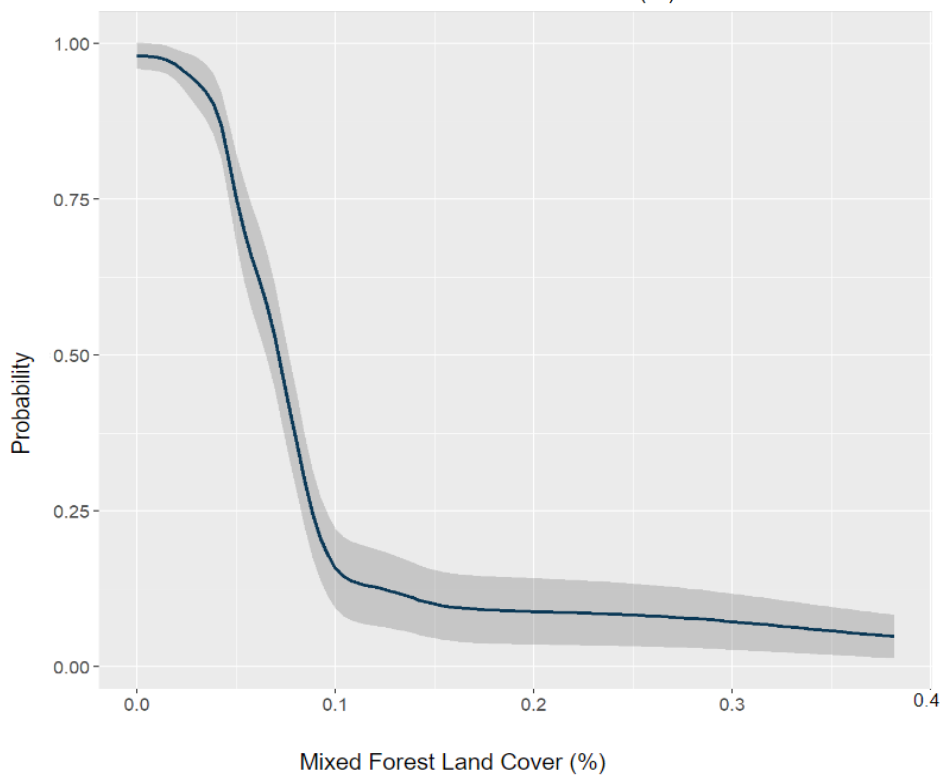
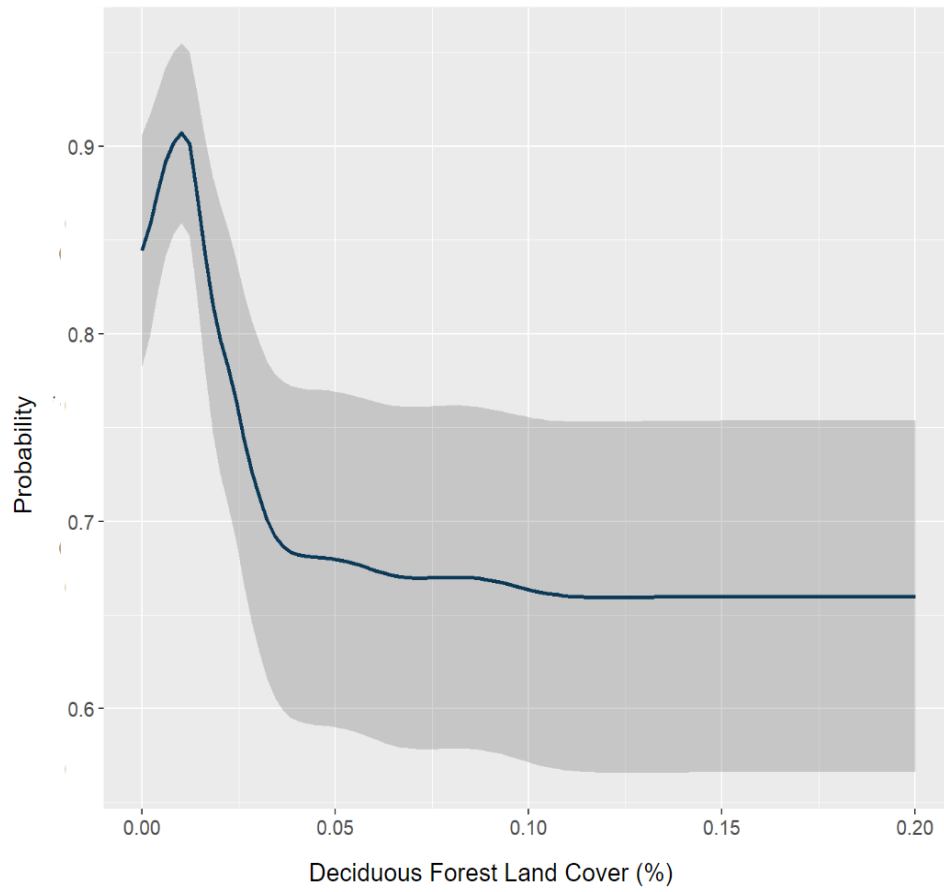
Figure B.2. Response curves of variable relationship with corresponding southern fox squirrel probability of use based on sdm modeling in the Coastal Plain region of Virginia, 2020-2022.

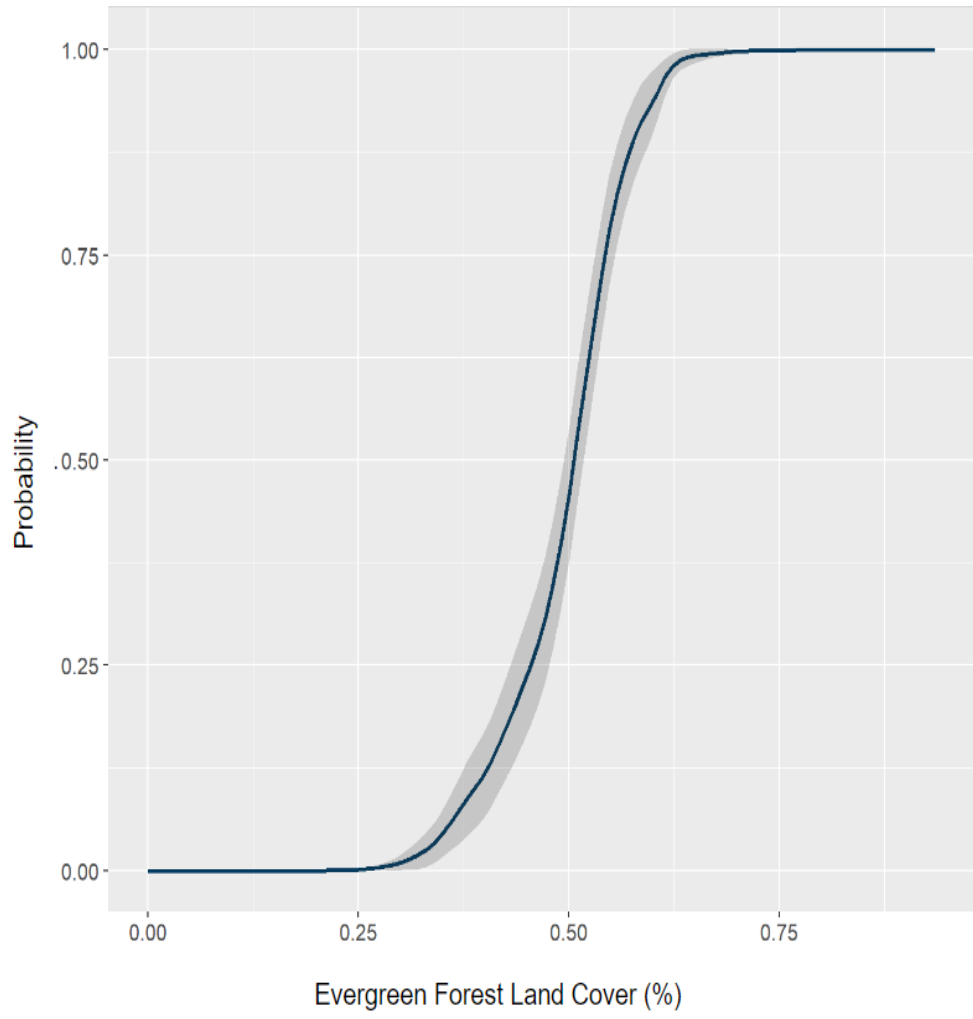












Appendix B: Literature Cited

- De La Cruz, J. and R. L. Ward. 2016. Summer-Habitat Suitability Modeling of *Myotis sodalis* (Indiana Bat) in the Eastern Mountains of West Virginia. *Northeastern Naturalist*. 23(1):100-117.
- Dewitz, J. and U.S. Geological Survey. 2022. National Land Cover Database (NLCD) 2019 (version 2.0). U.S. Geological Survey Data Release. <<https://www.sciencebase.gov/catalog/item/5f21cef582cef313ed940043>>. Accessed 16 May 2023.
- Greene, D.U. and R. A. McCleery. 2017. Multi-scale responses of fox squirrels to land-use changes in Florida: Utilization mimics historic pine savannas. *Forest Ecology and Management* 391:42-51.
- Hernandez, P.A., Graham, C.H., Master, L.L, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773-785.
- Jepsen, E.P.B., J.J. Keane, and H.B. Ernest. 2011. Winter distribution and conservation status of the Sierra Nevada Great Gray Owl. *Journal of Wildlife Management* 75:1678–1687.
- LANDFIRE. 2014. Vegetation disturbance layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- LANDFIRE. 2020a. Aspect layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- LANDFIRE. 2020b. DEM-Digital Elevation Model layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- LANDFIRE. 2020c. Slope Layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- LANDFIRE. 2022a. Forest canopy cover layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- LANDFIRE. 2022b. Fuel disturbance layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.

- LANDFIRE. 2022c. Fuel vegetation height layer. LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed online at <http://www.landfire/viewer>. Accessed 12 May 2023.
- Naimi, B. 2017. Usdm: Uncertainty Analysis of Species Distribution Models. Version 1.1-18. <<https://cran.r-project.org/web/packages/usdm>>. Accessed 6 October 2022.
- Naimi, B. and M. B. Aruajo. 2021. Species Distribution Modelling. R Package Version 1.1-8. <<https://cran.r-project.org/web/packages/sdm/sdm.pdf>> Accessed 12 May 2023.
- PRISM Climate Group. 2023. Data from recent years (1980-2022). PRISM Climate Group, Oregon State University. <<http://prism.oregonstate.edu>>. Accessed 12 May 2023.
- Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293.
- UCONN Center for Land Use Education and Research. 2023. CT Forest Fragmentation layer. University of Connecticut Center for Land Use Education and Research. <<https://clear.uconn.edu/projects/landscape/ct-forestfrag/>>. Accessed 12 May 2023.

Appendix C

**Examples of identified southern fox squirrels (*Sciurus niger niger*) from
remote trail camera locations**

**at Big Woods WMA, Piney Grove Preservation, and Military Training
Center Fort Barfoot, Virginia, October 2019- October 2020**

Figure C.1. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BWPG06, Piney Grove Preservation, Sussex County, Virginia, 2019



Figure C.2. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BWPG06, Piney Grove Preservation, Sussex County, Virginia, 2019



Figure C.3. Southern fox squirrel (*Sciurus niger niger*)- Location: Cam- BWPG12, Piney Grove Preservation (fixed date: 11/09/2019), Sussex County, Virginia, 2019



Figure C.4. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BWPG60, Piney Grove Preservation, Sussex County, Virginia, 2020



Figure C.5. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BWPG76, Big Woods Wildlife Management Area, Sussex County, Virginia, 2020 (fixed date: 4/30/2020)



Figure C.6. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BWPG142, Piney Grove Preservation, Sussex County, Virginia, 2020

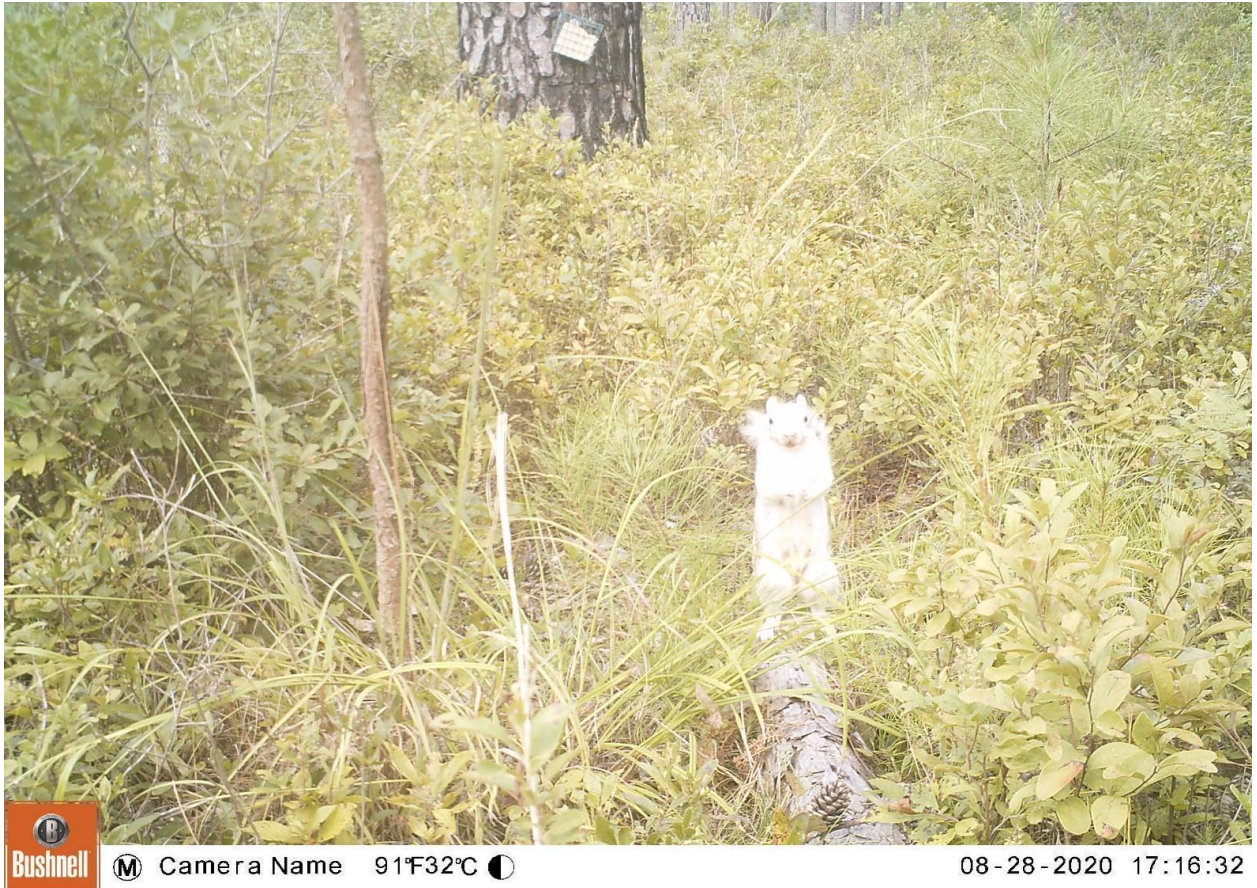


Figure C.7. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BOX_A, Piney Grove Preservation, Sussex County, Virginia, 2019



Figure C.8. Southern fox squirrel (*Sciurus niger niger*) - Location: Cam- BOX_C, Piney Grove Preservation, Sussex County, Virginia, 2020 (Fixed Date: 4/24/2020)



Appendix D

Examples of Identified Southern Fox Squirrels (*Sciurus niger niger*), Gray Squirrels (*Sciurus carolinensis*), Southern Flying Squirrels (*Glaucomys volans*) and other inhabitants from nest box locations

at Big Woods WMA, Piney Grove Preservation, and Military Training Center Fort Barfoot, November 2020- June 2022

Figure D.1. Eastern gray squirrel (*Sciurus carolinensis*)



Figure D.2. Eastern gray squirrels (*Sciurus carolinensis*), 2 individuals



Figure D.3. Eastern gray squirrel (*Sciurus carolinensis*) with two pups



Figure D.4. Southern flying squirrel (*Glaucomys volans*)

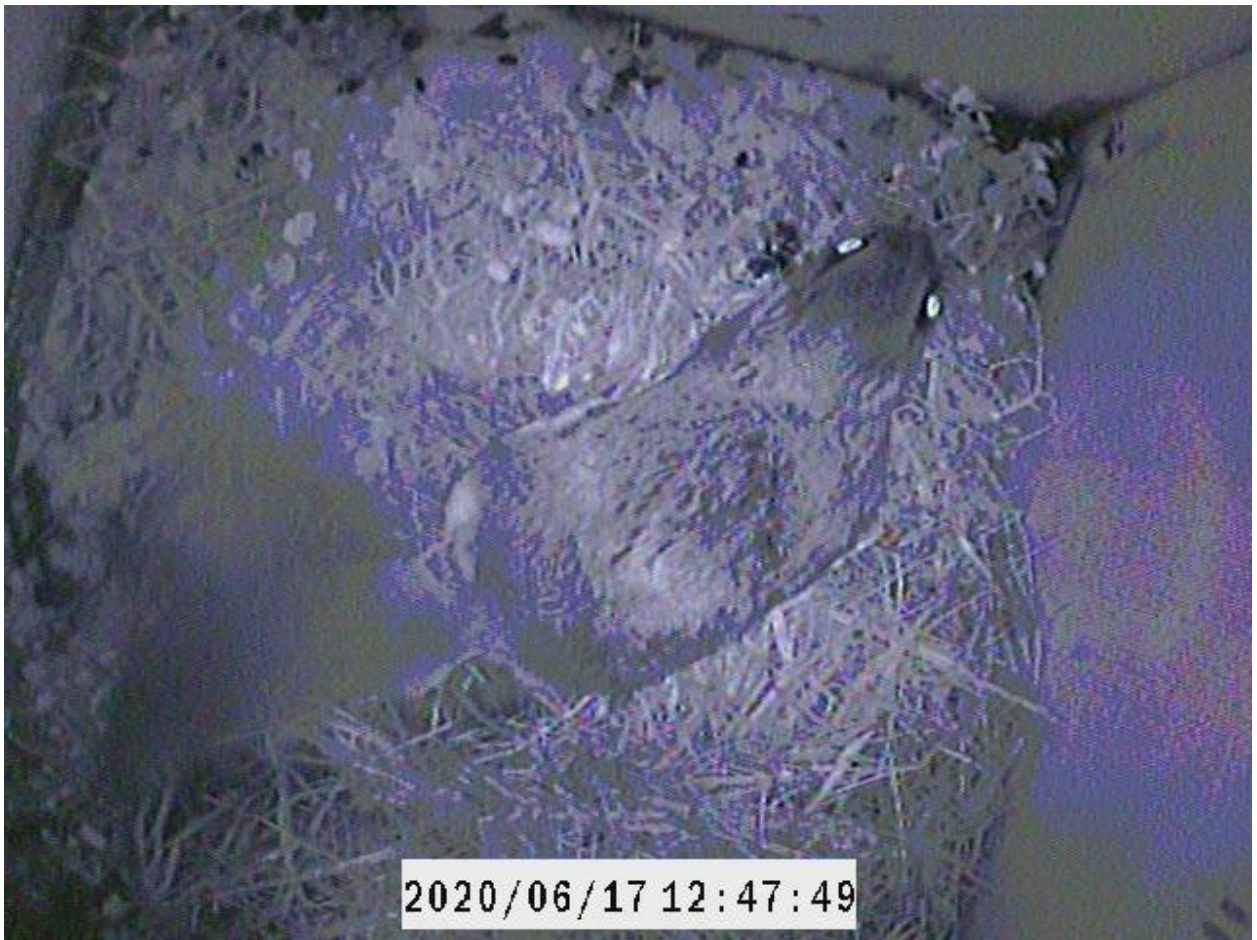


Figure D.5. Southern flying squirrel (*Glaucomys volans*), 3+ individuals



Other identified species in nest boxes:

Figure D.6. Eastern screech owl (*Megascops asio*)



Figure D.7. Eastern black rat snake (*Pantherophis alleghaniensis*)

