Southern Fox Squirrel and Eastern Gray Squirrel Interactions in a Fire-maintained Ecosystem

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Abstract: Southern fox squirrels (*Sciurus niger niger*) have been declining due to habitat fragmentation, cover type conversion, and fire suppression in the Southeast. A decrease in growing season burns has led to hardwood encroachment and forest mesophication that benefit the competing eastern gray squirrels (*S. carolinensis*). In the southern Coastal Plain and Piedmont of Virginia, these pattern raises the question of whether gray squirrels are competitively excluding southern fox squirrels in these altered landscapes. From October 2019 to October 2020, we conducted continual camera trapping for southern fox squirrels and gray squirrels on the Big Woods/Piney Grove Complex (BWPGC) and at Fort Barfoot (FB) in the Coastal Plain and lower Piedmont of Virginia, respectively. Both sites are among the few areas that still contain large, intact pine savanna and mixed-pine hardwood forests in southeastern Virginia. We used two-species occupancy modeling to investigate occupancy estimates of southern fox squirrels and possible competition with gray squirrels, based on detection histories collected from camera traps on BWPGC and FB. We then conducted informed single-species occupancy modeling to estimate the necessary level-of-effort (LOE) required to determine the probable absence of southern fox squirrels at sampling sites in the region. No fox squirrels were observed at FB. Our top, two-species occupancy model showed that gray squirrel occupancy increased with increasing time since last burn. However, southern fox squirrel occupancy, in the absence of gray squirrels, decreased with increasing time since last burn. Gray squirrels typically inhabited hardwood-dominant closed canopy areas whereas southern fox squirrels did so at BWPGC only in the absence of gray squirrels. This suggests that southern fox squirrels are selecting areas on BWPGC based on resource needs and possibly competition with gray squirrels. A single-season occupancy model confirmed that southern fox squirrel occupancy decreased with time since the last burn. Our LOE analysis indicated that seven consecutive days of camera trapping without a detection would provide 90% confidence of the subspecies' absence in areas burned two or more years prior to sampling. Southern fox squirrels may benefit from increased short-rotation burns to maintain or enhance pine-hardwood savannas and pine-hardwood savanna ecotones in southeastern Virginia.

Keywords: camera trapping, detection, occupancy, *Sciurus niger niger*

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The Coastal Plain of the southeastern U.S. has gone through major changes due to landscape conversions to agricultural or working forests for timber production (Weigl et al. 1989, Edwards et al. 2003, Edwards and Laerm 2007). Where pine savannas remain, natural disturbance regimes (i.e., frequent growing-season fire) have been replaced by fire suppression or at best, infrequent dormant season burning. Reduction of reoccurring, growing season fires often result in woody encroachment, and therefore changes in species composition, including open savanna specialists being replaced by generalists (Moorman et al. 2000).

Gray squirrels (*Sciurus carolinensis*) and southern fox squirrels (*S. niger niger*) are sympatric tree squirrels that co-exist across much of the southeastern U.S. despite having overlapping habitat needs for ecological traits such as foraging and nesting (Edwards et al. 2003, McRobie et al. 2019). Both species utilize mast from 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 species also use mature hardwood trees for drey nests or cavities as denning substrate (Koprowski 1994a, Koprowski 1995b, Edwards et al. 2003, Moncrief et al. 2012). However, across much of the southeastern U.S., fire suppression and forest mesophication have shifted forest structure and composition towards conditions that favor gray squirrels,

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which have a broader usable niche space compared to southern fox squirrels (Whitaker and Hamilton 1998, Nowacki and Abrams 2008, Sovie et al. 2020, Sovie et al. 2021).

Gray and fox squirrels appear to niche partition to minimize interspecific competition. 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). Gray squirrels and southern fox squirrels have also been known to show temporal partitioning across leaf-on and leaf-off seasons to minimize competition (Sovie et al 2019). Even with somewhat different habitat niches, competition among the two species is evident, particularly in hardwood areas (Sovie et al. 2020, Sovie et al. 2021).

We used two-species, single-season occupancy models to assess the effect of forest condition (e.g., basal area, canopy height), prescribed burn treatment (i.e., number of burns since 2017, time since last burn), and cover type classifications on occupancy of southern fox squirrels given selection and potential competition with gray squirrels. We also estimated camera-trapping level-of-effort (LOE) for detecting southern fox squirrels in southeastern Virginia using a single-species occupancy model assessing time since last burn (yr) informed by two-species occupancy modeling. Further, we assessed how environmental variables including time of year, daily precipitation, and daily average temperature affect southern fox squirrel detection probabilities. We predicted that southern fox squirrel occupancy probability would be greatest in recently burned areas of pine-hardwood mixed savanna in the absence of gray squirrels. We also predicted that fox squirrel detection would be negatively influenced by greater amounts of daily precipitation and extreme daily temperatures (high heat or freezing temperatures), as has been documented previously (Weigl et al. 1989).

Study Area

We conducted our study at the Virginia Army National Guard's Maneuver Training Center Fort Barfoot and the Big Woods Wildlife Management Area and Piney Grove Preserve Complex (BWPGC) managed by the Virginia Department of Wildlife Resources and the Nature Conservancy, respectively (Figure 1). Fort Barfoot (FB) is a 16,500-ha Virginia Army National Guard installation located in Nottoway, Dinwiddie, and Brunswick counties in the lower Piedmont province. The installation consists of a mixture of deciduous, pine, mixed pine-hardwood, and bottomland hardwood forests with open shrub and grassland areas throughout. Additionally, FB has a long history of fire-maintained disturbance (i.e., fire return intervals of 1–5 yr) over the past three decades

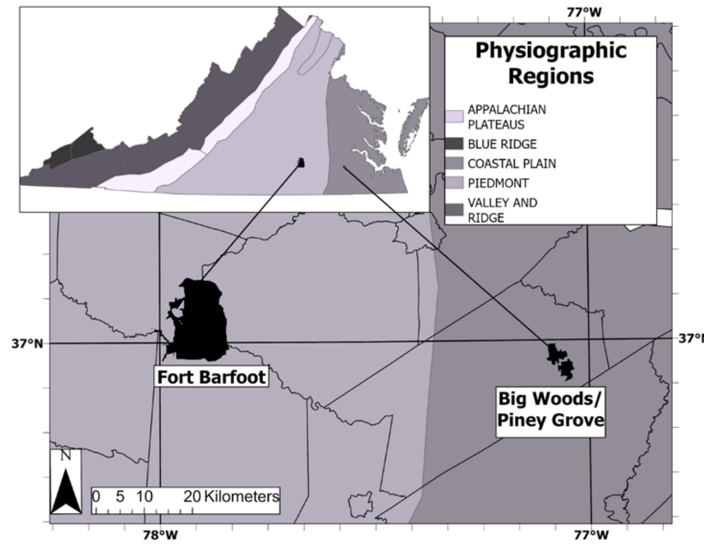

Figure 1. Southern fox squirrel (*Sciurus niger niger*) field sites, 2019–2022: Military Training Center Fort Barfoot, Nottoway County, Virginia (left) in the Piedmont region and the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County (right) in the Coastal Plain region.

that has helped maintain cover and structure approximating past natural conditions that are rare in the region (Kalen et al. 2014, Emrick et al. 2018). The BWPGC is in Sussex County in the upper Atlantic Coastal Plain and covers ~2100 ha. The cover types of this area are characterized by mixed loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*) stands, loblolly pine savannas, young longleaf (*P. palustris*) plantings, upland hardwoods, and bottomland hardwoods. Most of the complex, exclusive of the bottomland hardwoods, is managed with frequent fire (i.e., 2–3-yr fire return interval) to support populations of red-cockaded woodpecker (*Dryobates borealis*), northern bobwhite (*Colinus virginianus*), and eastern wild turkey (*Meleagris gallopavo silvestris*; Watts and Harding 2007). Since the early 2000s, burning has been used to manage red-cockaded woodpecker habitat. The BWPGC is one of the last remaining large, fire-maintained, mature pine savannas in southeastern Virginia (Bradshaw and Watts 2003).

Methods

Camera Surveys

We established trail camera survey points at FB and BWPGC to assess the presence of southern fox squirrels and gray squirrels following the methods of Tye et al. (2015), Greene et al. (2016), and Greene and McCleery (2017). Camera point selection was based on taking the boundary of the study areas, overlaying a systematic point grid, and then selecting random points that were evenly distributed among the main landcover types in ArcMap 10.8 (ERSI

Inc., Redlands, California). We stratified points using land cover as delineated by the National Land Cover Database, 2019 release (Dewitz and USGS 2022). Prior to final selection, we confirmed the presence of potential fox squirrel habitat through visual inspection against U.S. Department of Agriculture National Agriculture Imagery Program (NAIP) aerial imagery (2015, USDAFSA-APFO Aerial Photography Field Office, Salt Lake City, Utah) coupled with on-the-ground inspection, whereby points in unsuitable conditions such as water and buildings were avoided. We considered potential habitat as landcover important to southern fox squirrels elsewhere in the Southeast such as pine savannas, upland mixed pine-hardwood stands, and upland hardwood/hardwood bottomlands (Edwards et al. 1989, Edwards et al. 2003, Prince et al. 2014, Prince et al. 2016). Finally, we selected nine transect locations consisting of five cameras each based on the random points distributed in the potential southern fox squirrel habitat. We deployed trail cameras (Bushnell Trophy HD cameras, Bushnell Outdoor Products, Overland, Kansas) within the transects at approximately 250-m intervals to ensure independence of sample locations, as well as independence between camera survey transects (Tye et al. 2015).

Camera-trapping efforts at BWPGC were focused site's primary cover types: mature upland loblolly pine savannas, loblolly pine/hardwood forests, and bottomland hardwood-dominant riparian areas. At FB, we deployed camera transects in upland mixed loblolly pine/hardwood forests and upland loblolly pine forests to survey for potential presence of southern fox squirrels and in mature upland hardwood forests and bottomland hardwood forests that possibly could be occupied by eastern fox squirrels (*S. n. vulpinus;* Edwards et al. 1989, Edwards et al. 2003, Perkins and Conner 2004, Prince et al. 2014, Prince et al. 2016). We differentiated Sciurid species or subspecies based on pelage and size (Edwards et al. 2003, Edwards and Laerm 2007), although we note that the genetic foundation of fox squirrel sub-species categorization is questionable (Moncrief et al. 2010).

We deployed cameras from October 2019 to October 2020 on both BWPGC and FB. Due to equipment restraints, we deployed only three transects at a time for approximately 28 consecutive days. At the end of each 28-day rotation, we moved cameras to another grouping of three randomly chosen transect sites. We used three different rotations around the landscape for a total of nine randomly chosen transect locations. At each survey location, we 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. We 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). We then used DeerLab (2013, DeerLab, Inc. Jacksonville, Florida) to identify all observed mammals to species.

Predictor Variables

We considered six habitat covariates for two-species occupancy modeling (below): canopy cover, basal area, number of burns since 2017, time since last burn, canopy height, and general cover type (savanna vs. other). We considered these six 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 et al. 1988). Time since last burn and number of burns is important as prescribed fire has been deemed an important management tool for fox squirrel habitat in other parts of their range (Conner et al. 1999). These data were collected from land management records at both sites. Basal area and canopy cover (%) were collected in the field with a 10 basal area factor prism and concave spherical densiometer (Model-C, Forestry Suppliers, Jackson, MS) (Lemmon 1957). Both variables were used 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). Average canopy height was calculated using USGS 2014 LiDAR point clouds (VGIN 2016) and the package lidR (Roussel et al. 2020) in R (R Core Team 2022), as canopy height is positively correlated with fox squirrel presence (Conner and Godbois 2003). We then used a 50-m circular moving window analysis to find the focal mean of percent canopy height for all pixels across the landscape. The presence of savanna, also an important cover type for fox squirrels (Edwards et al. 2003), was considered as a covariate as BWPGC is mainly covered by loblolly pine woodland savannas. We 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). We then cut predictions based on a threshold that maximized sensitivity and specificity in relation to the training point classifications.

Data Analysis

We assessed the presence/absence of southern fox squirrels and eastern gray squirrels using occupancy analysis for both field sites. The sample interval reflected time between camera deployments (i.e., 28 days), with each day treated as a survey occasion. Our occupancy model sets included 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 2017, time since last burn), a canopy height model, and a general cover type model (1 as savanna; 0 as other cover types). To account for collinearity among our covariates, we used the package usdm (Naimi 2017) in R, where any variables with $r > 0.7$ were compared and the covariate with the least support was not included in our final analysis (Amspacher et al. 2019). We standardized all continuous variables (MacKenzie et al. 2006, Fiske and Chandler 2011) and created dummy variables for categorical variables prior to analysis. We used single-season, two-species occupancy to specifically assess the associations and possible competition of southern fox squirrels and gray squirrels. We then modeled survey effort using single-species occupancy and detection models informed by informative occupancy variables derived from two-species top modeling results.

We 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, 2021), we considered gray squirrels to be dominant and fox squirrels to be the subordinate species.

We focused on parameterization that assessed 1) ψCa: the probability of fox squirrel occupancy in absence of gray squirrels; 2) ψCA: the probability of fox squirrel occupancy in the presence of gray squirrels, and 3) ψA: the probability of gray squirrel occupancy. We concurrently assessed *a priori* models regarding the interactions of gray squirrels and southern fox squirrels when gray squirrels were absent (ψA:ψCa), and the interactions of gray squirrels and southern fox squirrels when gray squirrels are present (ψA:ψCA) for a total of 16 model interactions. Detection probably was modeled as constant (p[.]) for two-species occupancy modeling. Using Akaike's Information Criteria for small sample sizes (AIC_c), we considered models within 2 AIC_c units of the top models to be competing models (Burnham and Anderson 2002). Of the covariates in the top models, we considered covariates with 95% CI not crossing zero to be significant predictors of occupancy (Shake et al. 2011, Bowling et al. 2014).

We performed single-species modeling using the package wiqid in R (Meredith 2022) to test single-season, single-species occupancy (ψ) and detection (p) 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 (yr) to examine LOE relationships. We used the formula provided by Wintle et al. (2012),

$$n = \frac{log(\frac{\alpha}{1-\alpha}) - log(\frac{\psi}{1-\psi})}{log(1-p)}$$

where α is a desired confidence level, or range of theoretical probabilities, ψ is occupancy, and p 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 (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 (Weigl et al. 1989, Ditgen et al. 2007). Weather data were retrieved from the National Oceanic and Atmospheric Administration National Weather Station located in Wakefield, Virginia. Julian day was utilized on a 1–365 scale whereas (January 1–December 31). 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 (Edwards and Laerm 2007).

Results

From our efforts on October 2019 to October 2020, we recorded 370 trap days per camera point for a total effort of 16,650 trap days across all cameras in each transect for a total of 45 camera points at both BWPGC and FB. Within our entire survey period, we identified fox squirrels at 13 (29%) of the 45 camera points at BWPGC. Based on pelage and live captures from a concurrent radio-tracking study, along with the forest condition and composition, all fox squirrels at BWPGC were presumably the southern subspecies. Gray squirrels were identified at 17 (38%) of the 45 camera sites at BWPGC. Both southern fox squirrels and gray squirrels were detected on all landcover types on BWPGC (pine savanna, hardwood bottomland, young, managed pine, and hardwood-pine mixes). However, southern fox squirrels were typically detected at points located in pine savannas and gray squirrels were identified at points located in hardwood bottomlands. Southern fox and gray squirrels overlapped at only 2 (4%) of the 45 camera sites at BWPGC. At Fort Barfoot, we identified gray squirrels at 41 (91%) of the 45 camera sites. We did not detect either eastern or southern fox squirrels at FB over the study, therefore we limited occupancy and detection analyses for both species to BWPGC.

In assessing interactions among single-season, two-species occupancy modeling, our top model explaining the interaction of southern fox squirrels and gray squirrels was the influence of time since the last burn (ψA:ψCa; Table 1). Gray squirrel occupancy probability (ψA) increased the longer time persisted between burns (ψA $\beta_{\text{time since last burn}} = 0.75$, SE = 2.12). Moreover, in the absence of gray squirrels, southern fox squirrel occupancy probability (ψCa) decreased the longer time persisted between burns (ψCa $\beta_{\text{time since last burn}} = -1.44$, SE= 0.72; Figure 2).

We utilized the time since last burn covariate from our top, two-species occupancy model to inform LOE in surveying southern fox squirrels. For southern fox squirrels, our null for detection (constant p) had the most support (p[intercept] $\beta = -3.61$, SE = 0.18; Table 2). Our informed single-season occupancy model revealed that southern fox squirrel occupancy decreased with more years since last burn (ψ[Time since last burn] $\beta = -1.44$, SE = 0.72; Table 2). Furthermore, we estimated that the necessary LOE for sequential non-detections of southern fox squirrels would be 42 days for 1 yr since last burn, and 7 days for ≥2 yr since the last burn (Figure 3).

Table 1. Southern fox squirrel (*Sciurus niger niger*) two-species occupancy (ψA:Cψ) 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 ΔAIC < 2.0 from the top model.

Model[a]	AIC_c	ΔAIC_c	Model Likelihood	w_i
ψA:ψCa (Time since last burn)	964.63	0.00	1.000	0.777
ψA:ψCA (Time since last burn)	968.07	3.44	0.179	0.139
ψA:ψCa (.)	971.56	6.93	0.031	0.024
ψA:ψCa (Forest Condition)	972.44	7.81	0.020	0.016
ψA:ψCa (Savanna + Canopy Height)	972.90	8.27	0.016	0.012
ψA:ψCA (Forest Condition)	972.92	8.29	0.016	0.012
ψA:ψCA (.)	973.75	9.12	0.010	0.008
ψA:ψCa (Forest Condition + Savanna)	973.98	9.35	0.009	0.007
ψA:ψCA (Canopy Cover + Canopy Height)	974.48	9.85	0.007	0.006
ψA:ψCA (Forest Condition + Savanna)	975.23	10.61	0.005	0.004
ψA:ψCa (Canopy Cover + Canopy Height)	975.59	10.96	0.004	0.003
ψA:ψCa (Canopy Height)	975.69	11.06	0.004	0.003
ψA:ψCA (Savanna + Canopy Height)	976.12	11.49	0.003	0.002
ψA:ψCA (Canopy Height)	976.21	11.58	0.003	0.002
ψA:ψCa (Basal Area + Canopy Height)	977.77	13.14	0.001	0.001
ψA:ψCA (Basal Area + Canopy Height)	979.26	14.63	0.001	0.001

a. Detection modeled as p(.) in each model.

Table 2. Southern fox squirrel (*Sciurus niger niger*) single-species occupancy (ψ) and detection (p) 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 ΔAIC < 2.0 from the top model. Significant variables denoted by *.

Model	AIC_c	ΔAIC_c	LogLik	w_i
ψ (Time since last burn)*, p (.)	395.6	0.00	−194.5	0.48
ψ (Time since last burn)*, p (Julian day)	396.2	0.63	−193.6	0.35
ψ (Time since last burn)*, p (Precipitation)	397.8	2.16	−194.4	0.16
ψ (Time since last burn), p (Julian day + Precipitation)	422.7	27.11	−205.6	0.00
ψ (Time since last burn), p (Temperature + Precipitation + Julian day)	422.7	27.13	−204.2	0.00
ψ (Time since last burn), p (Julian day + Temperature)	428.0	32.38	−208.2	0.00
ψ (Time since last burn), p (Precipitation + Temperature)	428.9	33.34	−208.7	0.00
ψ (Time since last burn), p (Temperature)	453.2	57.60	−222.1	0.00

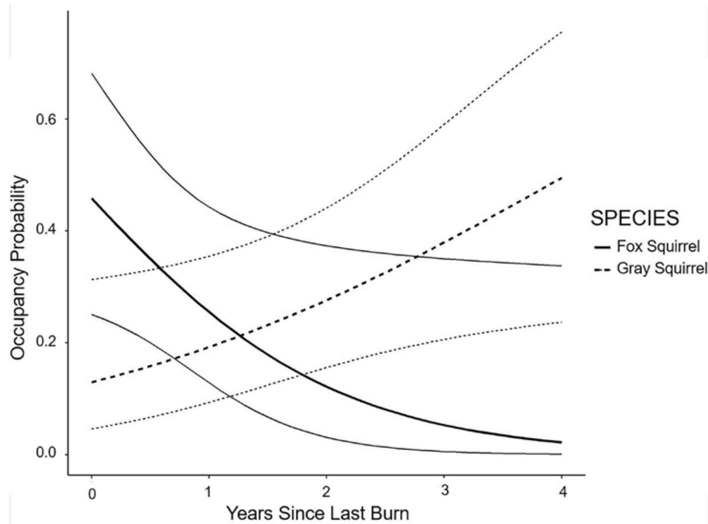

Figure 2. Effect of time since last burn (yr) for eastern gray squirrel (*Sciurus carolinensis*) occupancy (ψA) and southern fox squirrel (*Sciurus niger niger*) occupancy when gray squirrels are absent (ψCa) at remote trail camera locations on the Virginia Department of Wildlife Resources' Big Woods 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 from model ψA:ψCa (Time Since Burn), p(.). Dashed lines and solid black lines represent 95% confidence intervals for gray squirrels and fox squirrels, respectively.

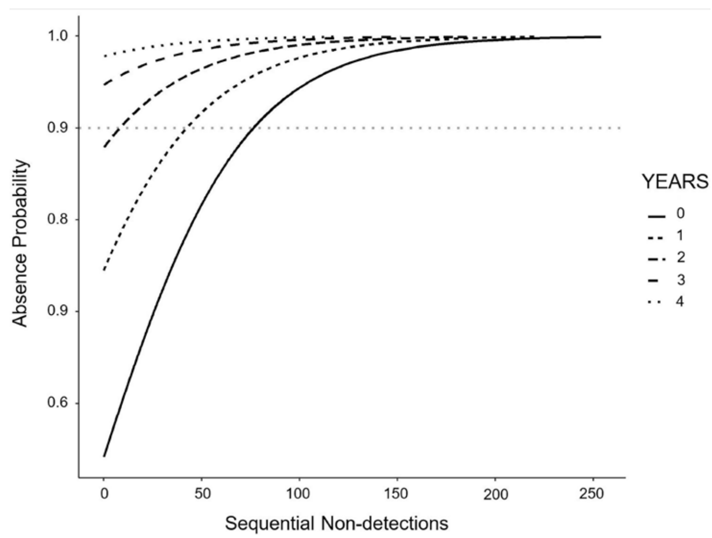

Figure 3. The total number of sequential non-detections required to determine the probable absence of southern fox squirrels (*Sciurus niger niger*) based on time since last burn (yr) and null detection, p(.) on the Virginia Department of Wildlife Resources' Big Woods Wildlife Management Area and Nature Conservancy's Piney Grove in Sussex County, Virginia, 2019–2020.

Discussion

Our results documenting southern fox squirrel and gray squirrel occupancy interactions indicate that, like elsewhere in the Southeast, fox squirrel occupancy increases with shorter prescribed fire rotational periods, particularly in the absence of gray squirrels (Parker and Nilon 2008, Steele and Koprowski 2011, Benson 2013, Sovie et al. 2021). Burned areas at BWPGC included pine savannas/woodlands, pine/hardwood forests, and the edges of bottomland hardwood. Gray squirrels more often inhabit areas of closed canopies that are characterized by hardwood dominant areas, particularly bottomlands, whereas southern fox squirrels only did so in the absence of gray squirrels (Gilliam and Platt 1999, Sovie et al. 2021). However, our top, two-species occupancy model indicated that southern fox squirrels occurred in frequently burned areas regardless of cover type as well as areas without gray squirrels. Our cover type classification for occupancy analysis was a binary scale (pine savanna vs. other cover type), where other cover types included hardwood bottomlands and hardwood/pine mixed stands. This suggests that fox squirrels responded to fire-maintained forest structure but also to potential competition with gray squirrels.

Interactions between two species is likely partly due to Interference competition, as gray squirrels are more aggressive and tend to discourage fox squirrels from areas of use (Wauters and Gurnell 2002, Sovie et al. 2021). Additionally, there could be an element of exploitative competition. Hardwoods in the upland system at BWPGC were limited in extent, and gray squirrels readily utilized most of the available hardwood patches and bottomlands that would be available to southern fox squirrels. However, parsing out these mechanistic aspects of competition at our study areas would require additional research.

Our analysis of southern fox squirrel detectability revealed that neither Julian day, average daily temperature, nor precipitation influenced detection probability In other areas of the Southeast, Ditgen et al. (2007) documented low squirrel activity in the hottest times of the year, while Pynne et al. (2020) detected no significant changes in squirrel activity based on average daily temperatures or precipitation, as we observed. Geographically, temperature extremes vary and may drive the activity of the subspecies differently among regions (Brown and Yeager 1945, Bakken 1959), as well as the temporal partitioning between gray squirrels and southern fox squirrels (Sovie et al. 2019), and seasonal activity shifts (Weigl et al. 1989, Edwards et al. 2003). Therefore, depending on the objective, the activity of fox squirrels can be driven by environmental variables as well as variables related to the ecology of the squirrel itself. To counteract any potential, yet poorly known, effects of environmental variables on detection probabilities, managers should utilize multi-day surveys throughout multiple seasons to account for any possible variation (Pynne et al. 2020).

Camera trapping efforts confirmed that, despite the presence of putative habitat, the probability of occurrence for southern fox squirrels at BWPGC is low to moderate, and therefore likely low to moderate densities, similar to current observations across much of the Southeast (Weigl et al. 1989, Loeb and Moncrief 1993, Edwards and Laerm 2007). Also, no fox squirrel subspecies was observed at FB despite anecdotal accounts of presence. Because our camera-trapping sessions exceeded the necessary LOE duration at most cameras at BWPGC and FB, we have high confidence that there are no established populations of fox squirrels of both subspecies at FB presently, though we note much of this large installation has yet to be surveyed. Our results from BWPGC suggest at least 7 camera-trapping days are required to determine probable absence of southern fox squirrels in stands burned at least 2 yr prior. Unfortunately, necessary effort greatly increases on newly burned sites as conditions immediately post-fire might not be conducive to fox squirrel detection at BWPGC, or detection decreases due to increases in home range as newly burned sites provide more available areas of use. Deeley et al. (2021) noted that maximizing the number of survey points rather than survey duration is often most optimal, assuming some broad understanding of level of effort needed. Accordingly, in southeastern Virginia, managers probably could survey with confidence for less than our 28-day periods at any given site thereby allowing more sites to be surveyed.

Our lack of detections of fox squirrels at FB may suggest that the lower Piedmont of Virginia has not yet been colonized from the Blue Ridge Mountains to the east or from the Coastal Plain. Fox squirrels that appear to be a southeastern subspecies are present at BWPGC, but much of the surrounding landscape is likely of marginal quality (i.e., intensive agriculture, dense working pine forests), hence populations therein may be somewhat isolated. Additional surveys are warranted in the Coastal Plain of Virginia to better define the regional distribution of fox squirrels.

We also found that southern fox squirrels use hardwood-pine mixed ecotones in the absence of gray squirrels. Therefore, for managers attempting vegetative restoration to improve habitat quality for fox squirrels, habitat is best achieved with short fire return intervals (i.e., 1–2 yr) that create these open canopy conditions and decrease excessive hardwood encroachment (or practices that mimic these conditions). Additionally, increasing hardwood sources in dispersed, small patches within mature pine savannas coupled with fire might benefit fox squirrels without overly benefiting gray squirrels. For managers interested in efficiently documenting the presence of southern fox squirrels in southeastern

Virginia, we suggest prioritizing initial camera surveys in forests with short fire return intervals where our findings suggest detection probability is high and necessary LOE is lower.

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