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Southern fox squirrel (Sciurus niger niger) translocation, occupancy, and foraging behaviors

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SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) TRANSLOCATION, OCCUPANCY, AND FORAGING BEHAVIORS

A thesis submitted to
the Graduate College of
Marshall University
In partial fulfillment of
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Master of Science
In
Biological Sciences: Organismal, Evolutionary
and Ecological Biology
by
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Approved by
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Marshall University
July 2018

APPROVAL OF THESIS

We, the faculty supervising the work of Katelyn Amspacher, affirm that the thesis, *Southern Fox Squirrel (Sciurus niger niger) Translocation, Occupancy, and Foraging Behaviors*, meets the high academic standards for original scholarship and creative work established by the Biological Sciences Program and the College of Science. This work also conforms to the editorial standards of our discipline and the Graduate College of Marshall University. With our signatures, we approve the manuscript for publication.

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ABSTRACT

Southern fox squirrels (SFSs) are habitat specialists within the longleaf pine ecosystem of the southeastern US whose populations are declining due to habitat fragmentation. Eastern gray squirrels (EGSs) are generalists found throughout the eastern US that have historically avoided competition with SFSs through habitat-partitioning. The purpose of this study was threefold: 1) use translocation as a conservation tool to establish a population of SFSs on Marine Corps Recruit Depot Parris Island (MCRDPI), South Carolina and monitor survival, home range size, and habitat use post-translocation, 2) estimate SFS density on Spring Island, SC and examine patterns of SFS and EGS occupancy, and 3) quantify foraging behaviors of sympatric SFSs and EGSs. I hypothesized: 1) annual survival of translocated SFSs on MCRDPI would be lower than established SFS populations, home ranges would be of similar size to those previously reported and habitat use would indicate preference for open-canopy savannas/woodlands, 2) decreased SFS density on Spring Island due to land use change, and 3) foraging behaviors of sympatric SFSs and EGSs would reflect historical habitat preferences. To test these hypotheses, I: 1) translocated 62 SFSs (31 male, 31 female) to MCRDPI and radio-telemetrically monitored them for ≥ 90 days, 2) established 20 stratified random points on Spring Island, used camera traps to sample for SFSs and EGSs, identified individual SFSs to estimate density, and used multi-season occupancy models to test the effects of fire frequency and canopy cover on occupancy, and the effects of daily temperature and precipitation on detection probability, and 3) used feed depots and time-lapse videography to record SFS and EGS foraging events, classifying head-up posture as vigilant and head-down posture as foraging. I found: 1) SFS annual survival rates were lower than established populations but similar to translocated populations; home ranges were similar to those previously reported; and SFSs preferred closed-canopy forests, 2) Spring Island SFS density is similar to density estimates from the 1990s; EGS occupancy is negatively associated with fire frequency; and EGS detection probability is negatively associated with maximum daily temperature, and 3) SFS foraging events were significantly longer than EGSs, but SFSs were also significantly more vigilant.

CHAPTER 1

SURVIVAL, HOME-RANGE SIZE, AND HABITAT USE OF TRANSLOCATED SOUTHERN FOX SQUIRRELS (*SCIURUS NIGER NIGER*) ON MARINE CORPS RECRUIT DEPOT PARRIS ISLAND, SOUTH CAROLINA

INTRODUCTION

Southern fox squirrels (*Sciurus niger niger*, SFS) have been historically tied to the longleaf pine (*Pinus palustris*) ecosystem of the Southeastern Coastal Plain (Weigl *et al.* 1989, Engstrom 1993). This imperiled ecosystem is characterized by an open canopy with a sparse, diverse understory that is maintained with fire (Engstrom 1993). Fire exclusion and human activity (*e.g.*, timber harvest and urbanization) have reduced the ecosystem to 3% of its original range (Frost 1993). Fragmentation of the ecosystem has contributed to population decline in many species associated with longleaf pine, including SFSs (Frost 1993, Weigl *et al.* 1989, Perkins and Conner 2004).

Translocation is a conservation tool used to re-establish or augment populations in suitable habitat (Griffith *et al.* 1989). Translocation was effectively used to reintroduce Delmarva fox squirrels (*Sciurus niger cinereus*) to restored habitat (Bendel and Therres 1994) and led to their delisting from the Endangered Species Act in 2015 (U.S. Fish and Wildlife Service Docket ID: FWS-R5-ES-2014-0021). Southern fox squirrel population declines have also been successfully mitigated using translocation (Dawson *et al*. 2009). Suitable habitat is crucial to successful translocation, but individuals must survive and establish within identified available habitat to form a self-sustaining population (Griffith *et al*. 1989).

Though populations have declined, SFSs are still locally abundant on some properties within their range and can serve as donors for translocation. Southern fox squirrels are often found in pine savannas and woodlands but in the absence of suitable naturalized habitats can be found in ruderal habitats that provide appropriate structure (Weigl *et al*. 1989, Meehan and Jodice 2010, Greene and McCleery 2017). Southern fox squirrel translocation requires significant trapping effort as the species is difficult to capture (Greene *et al.* 2016). In addition, high mortality rates post-translocation require multiple years of translocation for best success in establishing a breeding population (Dawson *et al.* 2009).

The purpose of this study was to mitigate SFS population decline using translocation to establish a new breeding population on Marine Corps Recruit Depot Parris Island (MCRDPI), South Carolina, and to monitor SFS survival, home-range size, and habitat use post release. I expected survival to be lower than that exhibited by naturally-occurring populations throughout the range of SFSs due to the stress of translocation. I expected home ranges to be similar in size to previously reported home ranges for the species, and that SFS would show preference for open-canopy savanna/woodlands given the species' association with the longleaf pine ecosystem. This study was important because it tested the use of translocation as a conservation tool and established a breeding population of SFSs that could serve as a donor population for future conservation efforts.

METHODS

STUDY ORGANISM

Southern fox squirrels exhibit life history strategies that could contribute to the species' inability to rebound from population declines. Southern fox squirrels are one of ten subspecies of the eastern fox squirrel (*Sciurus niger*), and one of the largest and most ground dwelling of all North American tree squirrels (Weigl *et al.* 1989). They are relatively long-lived (longevity ~ 7-10 years) and are typically found in low densities (average 0.05-0.35 SFSs/hectare, Weigl *et al*.

1989). The main breeding season ranges from December to February, when each female has just one day of estrus (Weigl *et al.* 1989). After a 44-day gestation period, females give birth to an average 2.5 pups, one of the smallest litter sizes of all North American tree squirrels (Gurnell 1983, Weigl *et al*. 1989). Though rare, females breed again in late summer when food resources are adequate throughout the year (Weigl *et al.* 1989).

STUDY AREA

The MCRDPI, South Carolina is an active military base that trains thousands of Marine Corps recruits annually. The MCRDPI is a 3,220-ha sea island with approximately half of that acreage comprised of hard marsh. The MCRDPI has an active pine savanna restoration program that uses prescribed fire, mechanical thinning, and herbicides to manage wildlife habitat. Open-canopy pine savanna/woodlands, closed-canopy pine forests, and closed-canopy pine-hardwood forests are interspersed with a manicured golf course, training areas, and lawns. The MCRDPI had no SFS population prior to this study, but it is within the historic range of the species, and neighboring sea islands support stable populations (Lee *et al.* 2008).

CAPTURE/RADIO TELEMETRY

I trapped SFSs between January 2016 and June 2017 at five donor sites (Figure 1) using Mosby-style wooden box traps (Day *et al*. 1980) baited with pecans. Once captured, I transferred squirrels to a wire and canvas handling cone to determine sex and to estimate reproductive maturity. I immediately released lactating females, allowing them to return to their nests. I placed SFSs selected for translocation in covered, wire Havahart traps (Woodstream Corp., Litiz, PA) and transported them to Sea Island Animal Hospital (Lady's Island, SC) to be anesthetized with 20-30 mg of ketamine hydrochloride plus 1 mg acepromazine and fitted with radio collars (Advanced Telemetry Systems, Inc., Isanti, MN, Model M1640, 6.5g). I allowed SFSs at least three hours to recover from anesthesia before I hard released them in a live oak (*Quercus virginiana*) grove on the MCRDPI golf course. I selected this release site because of the prevalence of SFSs on golf courses in coastal South Carolina (Meehan and Jodice 2010).

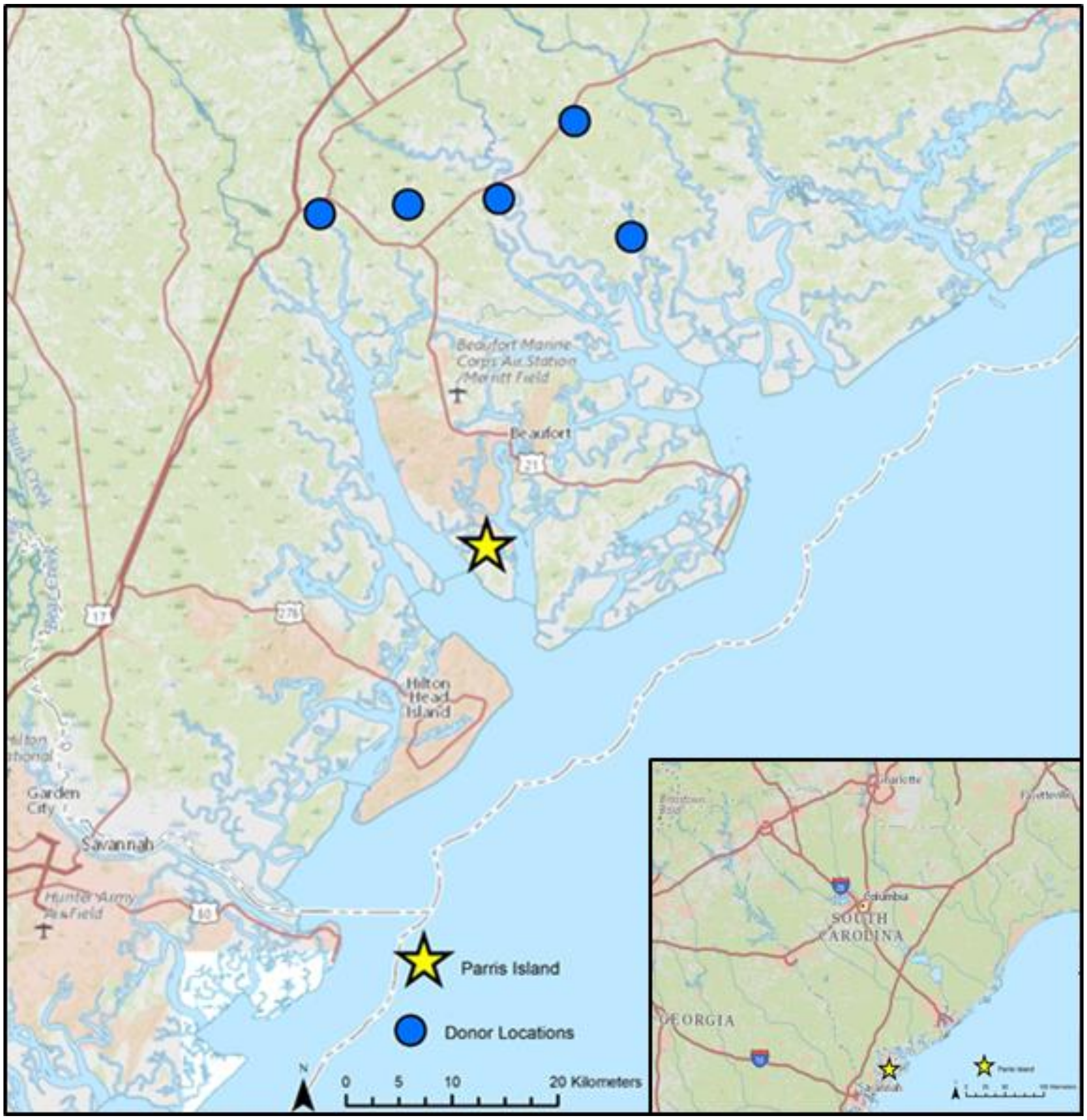

Figure 1. Map of Donor Locations and Translocation Site
Southern fox squirrels were trapped at five donor sites (blue dot) and translocated to Marine Corps Recruit Depot Parris Island (yellow star) between January 2016 and June 2017.

I radio-located SFSs at least twice weekly using a radio receiver (Advanced Telemetry Systems, Inc., R4000) and Yagi antenna for ≥ 90 days following release. I recorded SFS radio locations using a Trimble Juno 3 GPS unit (Trimble Inc., Sunnyvale, CA), and recorded weather data (*e.g.*, wind, rain, and temperature), habitat and positional data (*e.g.*, tree type and location in/around tree), and activity data (*e.g.*, foraging and social) at each location.

STATISTICAL ANALYSIS

Survival. I used known-fate models in program MARK (White and Burnham 1999) to examine monthly SFS survival post translocation from January 2016 to September 2017. I left-censored individuals before their release date and right-censored individuals after collar batteries died. I formatted the encounter history file to include one live/dead entry per month for twelve months (*i.e.*, twelve entries), and created two entries for SFSs present on MCRDPI in both 2016 and 2017.

I constructed four candidate models to examine covariate performance and one constant survival model (Table 1). I used the covariate cohort to define which year the SFS was translocated and the covariate year to define which year the encounter history was recorded. I also used sex and mass (z-standardized) as covariates of survival. I ranked models with Akaike's information criterion (AIC) adjusted for small sample size with AIC_C (Akaike 1973, Burnham and Anderson 2002).

Table 1. Survival Models
Survival models ranked according to AICc model selection. Supported model (ΔAICc < 2.0) indicated by *.

Model	AIC_C	ΔAIC_C	ω_i	k	Likelihood	Deviance
S(cohort)*	204.2854	0.0000	0.33298	2	1.000	200.2546
S(year)	217.6341	13.3487	0.00042	2	0.0013	213.6033
S(sex)	218.1587	13.8733	0.00032	2	0.0010	214.1280
S(.)	218.9670	14.6816	0.00022	1	0.0007	216.9567
S(mass)	220.3281	16.0427	0.00011	2	0.0003	216.2973

Habitat Use. I used package adehabitatHR (Calenge 2006) in Program R (R Core Team 2018) to calculate 85% minimum convex polygon core home ranges appropriate for tree squirrels (Wauters *et al*. 2007) for those SFSs that had ≥ 30 data points (n = 27). I classified habitat for 2015 and 2017, but did not include 2016 due to damage and salvage cuts from Hurricane Matthew in fall 2016. I classified habitat into four categories: manicured, marsh, closed-canopy forest, and open-canopy savanna/woodlands. I established structure-based habitat classes because of the prevalence of SFSs on golf courses and in anthropogenic areas nearby (Lee *et al*. 2008, Meehan and Jodice 2010), and the availability of both anthropogenic and naturalized areas with suitable structure on MCRDPI (Greene and McCleery 2017). I obtained 9-inch resolution imagery from the Beaufort County, SC GIS department to hand-digitize canopy cover, marsh, and manicured areas (mowed/maintained) on MCRDPI using Raster Paint in ArcGIS (Esri, Redlands, CA). I used focal statistics in the neighborhood toolset to determine canopy cover at a 20-m scale and classified wooded pixels with ≥ 70% canopy cover as closed-canopy forest, and < 70% canopy cover as open-canopy savanna/woodlands (Figures 2 & 3). I used the shrink tool in ArcGIS to apply a 10.5m edge effect to forested areas using a 7-cell shrink.

I evaluated SFS habitat use with use versus availability analysis. I generated 90 random points within each home range (n = 2224) and tied them to 180 random points at the landscape scale (n = 4783) but removed any points that fell in ponds or on roads/rooftops. I used binomial logistic regression (PROC GLIMMIX) in SAS (SAS Institute, Cary, NC) to test habitat type as a function of use at Johnson's 2nd order of habitat selection (Johnson 1980). I treated squirrel as a random effect in the analysis to account for a lack of independence among observations from the same individual.

Figure 2. Marine Corps Recruit Depot Parris Island 2015 Habitat Classification
Classified habitats of Marine Corps Recruit Depot Parris Island in 2015. Anthropogenic and water were not considered as southern fox squirrel habitat in use versus availability analysis.

Figure 3. Marine Corps Recruit Depot Parris Island 2017 Habitat Classification
Classified habitats of Marine Corps Recruit Depot Parris Island in 2017. Anthropogenic and water were not considered as southern fox squirrel habitat in use versus availability analysis.

RESULTS

I trapped and translocated 62 squirrels (31 male, 31 female) to MCRDPI between January 2016 and June 2017 in < 1,200 trap nights. Trap success was greater at anthropogenic sites (22.3%) than naturalized sites (5.6%). I recovered 31 SFSs that died as a result of predation (*e.g.*, red-tail hawks (11), eastern diamondback rattlesnakes (5), great horned owls (4), and bobcats (2); n = 22), vehicular strikes (n = 1), and unknown causes (n = 8). Only the cohort survival model received support (Table 1), indicating survival was negatively associated with cohort (β = -1.57 ± 0.40, 95% CI: -2.36 – -0.79, Figure 4). Annual survival probability was higher for the 2016 cohort (0.63 ± 0.09) than for the 2017 cohort (0.12 ± 0.06). Monthly SFS survival averaged 0.92 ± 0.01, and average annual survival was 0.39 ± 0.07.

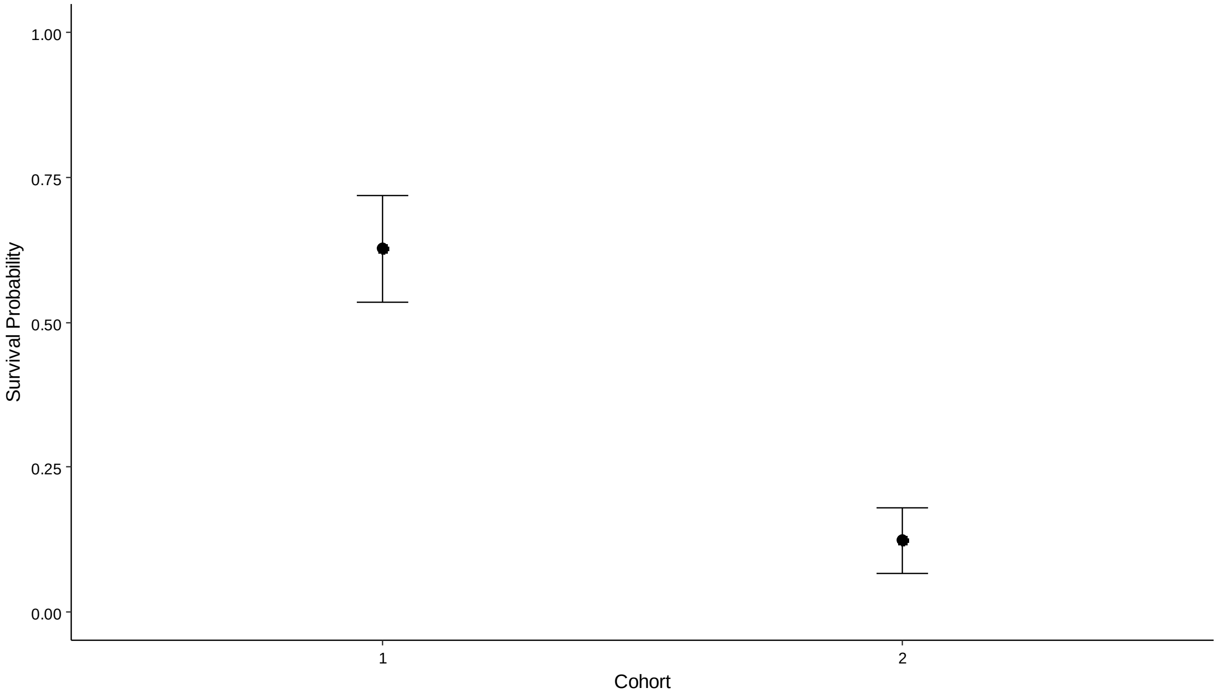

Figure 4. Southern Fox Squirrel Survival by Cohort
Southern fox squirrel survival by cohort. Cohort one was telemetrically monitored beginning in January 2016, and cohort 2 was telemetrically monitored beginning in January 2017.

Translocated SFS home ranges averaged 32.1 ha (SD = 54.8). Female home ranges averaged 6.6 ha (SD = 4.0) and male home ranges averaged 49.7 ha (SD = 65.6). At the home-range scale, SFSs preferred closed-canopy forest over all other habitat classes, and model fit was acceptable (Pearson $\chi 2/\mathrm{df} = 0.97$, Table 2). Odds ratios indicated that SFSs were 1.8, 8.9, and 22.2 times more likely to use closed-canopy forest than open-canopy savanna/woodlands, manicured areas, and marsh, respectively (Table 2).

Table 2. Habitat Use Parameter Estimates
Parameter estimates and 95% confidence intervals for SFS habitat use at the home-range scale. Closed-canopy forest was used as the reference habitat category. SE = standard error, LCL = 95% lower confidence limit, UCL = 95% upper confidence limit, Odds = odds of using closed-canopy forest compared to other habitat classes.

Parameter	Estimate	SE	LCL	UCL	P > |t|	Odds
Manicured	-2.1907	0.1079	-2.4022	-1.9793	< 0.0001	8.9
Marsh	-3.0963	0.1089	-3.3098	-2.8829	< 0.0001	22.2
Savanna/woodland	-0.5655	0.08508	-0.7323	-0.3987	< 0.0001	1.8

DISCUSSION

My survival analysis supported the hypothesis that survival of translocated SFSs would be lower than established populations. However, survival estimates from this translocation study were similar to estimates from other successful translocations (Table 3). I released both cohorts of SFSs at the same location, so the difference between 2016 and 2017 cohorts could reflect increased predator awareness of the new food source or increased predator populations.

Table 3. Southern Fox Squirrel Annual Survival
Comparison of southern fox squirrel annual survival in established and translocated populations.

Treatment/Location	**Annual Survival**	**Source**
Established		
Fort Bragg, NC	0.49	Prince *et al.* 2014
Spring Island, SC	0.62	Lee *et al.* 2008
Ichauway, GA	0.69	Conner 2001
Translocated		
Parris Island, SC	0.39	Current study
St. Phillips Island, SC	0.71	Dawson *et al.* 2009
Hall Island, SC	0.34	Dawson *et al.* 2009

Hard release translocation techniques are associated with immediate dispersal from the release site, increased movement, and decreased survival in most species (Bright and Morris 1994). I found 84% of the 31 recovered SFSs dead within 90 days of translocation. Most of the SFS deaths in this study were attributed to predation, therefore indicating reduced vigilance immediately after release. Bendel and Therres (1994) used a soft-release technique but also reported a high percentage (78%) of overall deaths during the first 90 days post translocation. The high percentage of deaths in both studies suggests that translocated individuals may exhibit riskier behavior immediately after release, regardless of release technique, making them more vulnerable to predators. Future translocations should consider releasing animals at a different location during the second year to avoid predator concentration on translocated individuals when they are most vulnerable.

Southern fox squirrel home ranges in this study supported my hypothesis that post translocation home ranges would be comparable to previously reported home ranges for the species (Table 4). However, my hypothesis that SFSs would prefer open-canopy savanna/woodlands at the home-range scale was not supported. I expected SFSs to prefer savanna/woodland structure due to their association with the longleaf pine ecosystem (Weigl *et al.* 1989, Engstrom 1993), but SFSs were 1.8 times more likely to use closed-canopy forest than open-canopy savanna/woodlands (Table 2). However, SFSs used both closed- and open-canopy habitats proportionately more than was available in the landscape, and increased use of open-canopy habitats after damage and salvage cuts from Hurricane Matthew increased available open-canopy savannas/woodlands (Figure 5).

Table 4. Southern Fox Squirrel Home Ranges
Comparison of reported southern fox squirrel home range sizes in hectares.

Location	Female	Male	Average	Source
Fort Bragg, NC[a]	19.83 ± 3.01	81.26 ± 14.12	36.7 ± 1.3	Prince *et al.* 2014
Ichauway, GA[b]	21.0 ± 6.3	37.0 ± 3.6	--	Conner 2000
St. Phillips Island,SC[c]	18.7 ± 5.6	16.5 ± 6.0	--	Dawson *et al.* 2009
Hall Island, SC[c]	5.8 ± 0.7	147.8 ± 21.9	--	Dawson *et al.* 2009
Southeastern NC[c]	17.2	26.6	17.9	Weigl *et al.* 1989
Parris Island, SC[d]	6.6 ± 1.2	49.7 ± 16.4	32.1 ± 10.5	Current Study

[a] 99% kernel-density [b] 95% kernel-density [c] 100% minimum convex polygon
[d] 85% minimum convex polygon

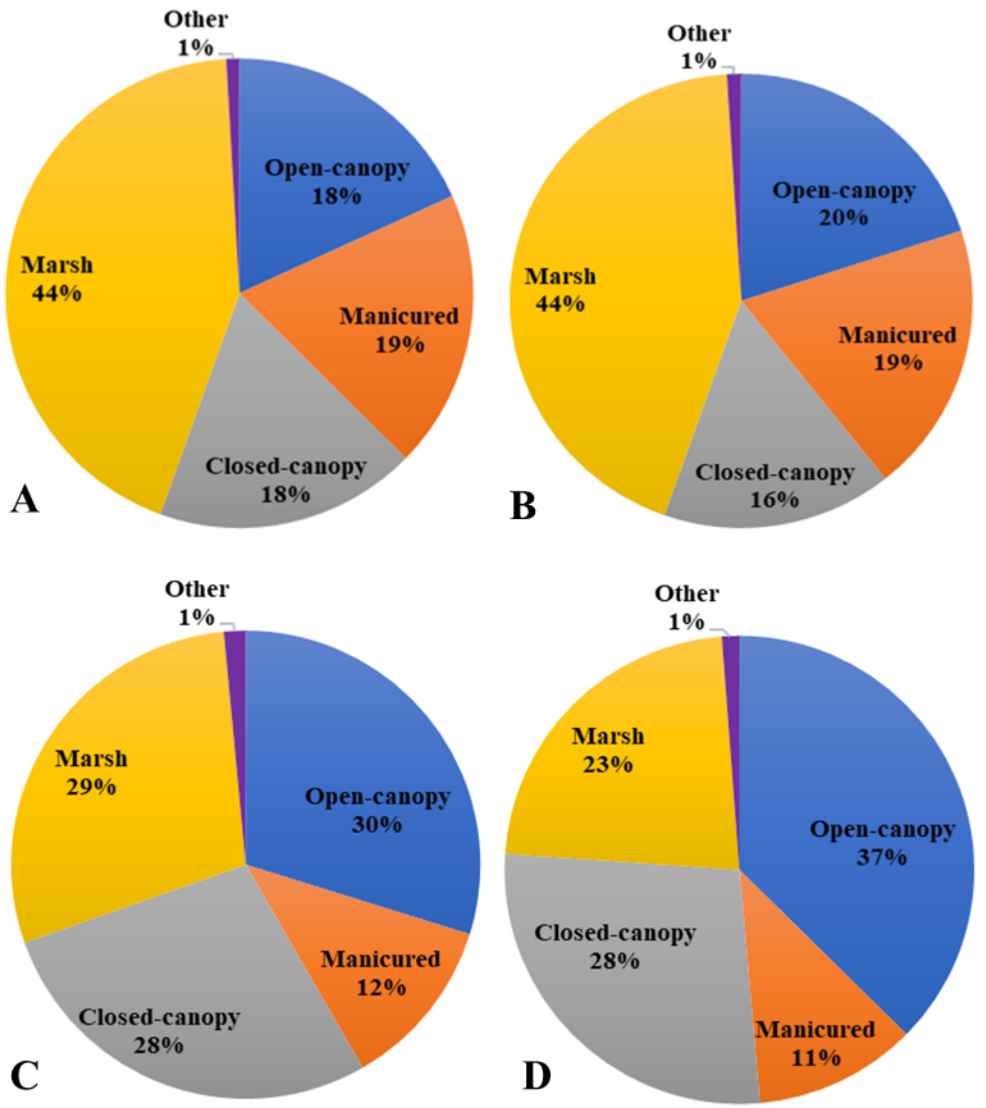

Figure 5. Habitat Class Proportions at the Landscape and Home Range Scales
Proportion of habitat classes in A) pre-hurricane landscape scale, B) post-hurricane landscape scale, C) pre-hurricane home range scale, and D) post-hurricane home range scale.

Sherman's fox squirrels (*Sciurus niger shermani*) are associated with open-canopy systems at the landscape scale, but with increasingly closed canopy indicative of hardwood "runners" at fine scales ≤ 5.3 ha (Greene and McCleery 2017). Southern fox squirrels use patches of closed-canopy hardwoods within open-canopy pine savannas and woodlands for refugia, nesting, and cover from predators (Conner and Godbois 2003, McCleery 2009). Home ranges in this study ranged from 0.5 to 220.6 ha, and nearly half were less than 5.3 ha. Home range analysis included points during the first 90 days post-translocation when individuals may exhibit aberrant behavior, and I used homing techniques to track SFSs which may have chased SFSs to trees and biased my results towards closed-canopy forests. Therefore, the preference for closed canopy in this study could be influenced by small home range size and behavioral effects of translocation and radio telemetry.

My habitat analysis did not consider understory structure, but open understories are important to SFSs that spend significant time on the ground (Weigl *et al*. 1989, Greene and McCleery 2017). The restoration process on MCRDPI is ongoing and some areas with a closed canopy have managed, open understories to facilitate military training. Thus, closed canopy forest is not necessarily indicative of dense forest on MCRDPI. Further research should investigate habitat preference using understory structure to gain a better understanding of how this translocated SFS population is using the landscape.

Annual survival and home-range size in this study were similar to previous successful translocations (Dawson *et al*. 2009). I observed several signs of SFS reproduction during the winter 2016/spring 2017 breeding season (*e.g.,* mating chases, active nests, young SFSs). These data suggest that this was a successful translocation that established a breeding population of SFSs on MCRDPI and support the use of translocation as a successful conservation tool to mitigate SFS declines.

CHAPTER 2

DIURNAL PATTERNS, OCCUPANCY, AND DETECTION OF SYMPATRIC SOUTHERN FOX SQUIRRELS (*SCIURUS NIGER NIGER*) AND EASTERN GRAY SQUIRRELS (*S. CAROLINENSIS*) AND SOUTHERN FOX SQUIRREL DENSITY ON SPRING ISLAND, SOUTH CAROLINA

INTRODUCTION

Species that are closely related and ecologically similar often have some niche dimension that differentiates them (Brown 1984). The niche breadth of specialist species is narrower than the niche breadth of generalist species, making specialists more vulnerable to habitat alterations (Brown 1984, Vázquez and Simberloff 2002, Wilson *et al.* 2008). Furthermore, generalist species typically adapt to human-altered landscapes better than specialist species (Swihart *et al.* 2003). Southern fox squirrels (*Sciurus niger niger*, SFS) and eastern gray squirrels (*S. carolinensis*, EGS) are closely related, sympatric specialist and generalist species that rely on habitat partitioning to limit competition (Weigl *et al.* 1989, Edwards *et al*. 1998).

Eastern gray squirrels are habitat generalists found in dense forests with woody groundcover throughout the eastern United States (Edwards *et al*. 1998). They typically live 8-9 years and frequently have 2 litters per year with an average 2.6 pups per litter (Barkalow *et al*. 1970). In addition, EGSs are often very abundant and reach high densities of up to 15 squirrels per hectare (Gurnell 1983).

Southern fox squirrels are habitat specialists associated with fire-maintained pine savannas and woodlands of the southeastern United States that have experienced population declines throughout their range due to habitat loss and fragmentation (Weigl *et al*. 1989, Perkins and Conner 2004). Southern fox squirrel life history might contribute to the species' inability to rebound from population declines. Southern fox squirrels are one of the largest and most ground dwelling of all North American tree squirrels (Weigl *et al.* 1989). They are relatively long-lived (longevity ~ 7-10 years) and typically have just one litter per year with an average 2.5 pups, which suggests they are a k-selected species (Weigl *et al*. 1989, Tappe and Guynn 1998). Additionally, SFSs are normally found in low densities (less than 0.35 SFS/ha, Weigl *et al*. 1989).

Spring Island, South Carolina reportedly supported the densest SFS population in the southeast during the 1990s (Lee 1999), but residents reported decreased SFS populations and increased EGS populations in the 2010s (C. Marsh and T. Mills, Spring Island Trust, pers. comm.). The purpose of this study was to evaluate the population changes on Spring Island using game cameras to estimate SFS density, and occupancy models to examine the influence of habitat structure and management technique (*e.g.*, prescribed fire frequency) on SFSs and EGSs occurrence. I hypothesized that decreased SFS density would be associated with the shift in land use from quail plantation to nature preserve/residential community in the early 1990s (Lee *et al*. 2008). I expected that this shift in land use led to a subsequent shift in habitat management, limiting prescribed fire prevalence, altering habitat structure, and allowing EGSs to encroach on SFS habitat. I hypothesized that habitat alterations limited the ability of SFSs and EGSs to partition habitat, leading to temporal partitioning instead. I expected EGS site occupancy to be greater than SFS site occupancy because EGSs are generalists, and SFS occupancy to be positively associated with fire frequency and negatively associated with canopy cover because of their association with the longleaf pine ecosystem. I expected detection probability of SFSs and EGSs to be similar because they are closely related species, and to be negatively associated with maximum daily temperature and daily precipitation because of reduced activity in heat and heavy rain.

METHODS

STUDY AREA

Spring Island is a 1200-ha sea island in South Carolina. The island was managed as a quail plantation from the mid-1900s until 1990 when it was sold for development. Quail plantation managers have used frequent, low-intensity prescribed fire to maintain large tracts of low-basal area pine/hardwoods with an open, diverse understory since Stoddard (1931) emphasized the importance of fire for quail (Moser *et al*. 2002, Van Lear *et al.* 2005). Management with frequent, low-intensity fire also provided habitat for other species of interest such as red-cockaded woodpeckers (*Picoides borealis*) and SFSs (Moser *et al*. 2002). Development on Spring Island led to increased human activity and road construction which fragmented the landscape and introduced a new source of mortality for SFSs (Lee *et al.* 2008). Spring Island is now considered an environmentally-friendly community with low-density housing for 400 families along the perimeter of the island hidden behind dense vegetation to maintain privacy. Spring Island features a golf course, clay range, sports complex, and farm for the enjoyment of residents. The Spring Island Trust was established to protect the environmental and cultural history of the island and maintain the 445 hectares in nature preserves. The Spring Island Trust and Spring Island Property Owners Association stress the importance of environmentally-sensitive development and the maintenance of Spring Island as a residential community within a nature preserve.

DATA COLLECTION

I used historic landcover classifications (Lee 1999) and current satellite imagery to establish 20 stratified random points on Spring Island, SC. I set 250 m as the minimum distance between random points (Tye *et al.* 2015). I used a convex spherical crown densiometer to measure canopy cover at each point in early June 2016 when sites were established (Forestry Suppliers, Inc., Jackson, MS). I digitized and georeferenced 25 years of historical prescribed burn maps from 1992 to 2017 using ArcGIS (Esri, Redlands, CA) and calculated the average number of times each point was burned during a five-year period to reflect historical fire return intervals (Stambaugh *et al.* 2011). I placed a game camera (Bushnell 14 MP Trophy Cam HD Aggressor, Bushnell Outdoor Products, Overland Park, KS) 70 cm above ground and 1.5 m from a pecan/corn bait pile (~ 19 liters) at each point and set cameras to take three pictures every 10 seconds (Tye *et al.* 2015). I visited cameras every other day to change SD cards and replenish bait. I ran cameras from June 24-30, 2016 and from April 20-26, 2017.

STATISTICAL ANALYSIS

Density and Diurnal Patterns. I calculated the area sampled using a 125 m (half the minimum distance between points) radius around each point. I identified individual SFSs from photographs using unique pelage characteristics (Tye *et al*. 2015). I divided the number of individuals identified by the area sampled to estimate SFS density. I used package camtrapR (Niedballa *et al.* 2017) in Program R (R Core Team 2018) to catalogue photographs and create a record table with entries for both EGSs and SFSs. I formatted the record table to only include records of the same species at the same station with at least 30 minutes between photographs to maintain independence between records. I used this record table to calculate kernel density diel activity overlap between EGSs and SFSs using the overlap coefficient Dhat1 (Ridout and Linkie 2009).

Occupancy. I used single-species multi-season occupancy models in program PRESENCE (MacKenzie *et al*. 2002) to identify patterns of occupancy and detection for both SFSs and EGSs. I assumed constant local extinction (ε) and colonization (γ) for all models. I formatted encounter history with two seasons (2016 and 2017) and seven replicates per season (14 total replicates) for each random point. The SFS multi-season model was of poor fit, so I adjusted SFS occupancy analysis to two, single-species single-season occupancy models. I retrieved maximum daily temperature and daily precipitation data from the National Oceanic and Atmospheric Administration (NOAA) station at the Marine Corps Air Station Beaufort (38.6 kilometers from Spring Island) and incorporated the data in models as detection covariates (Table 5). I used canopy cover and burn frequency as covariates of occupancy (Table 5). I used Spearman rho correlation to examine collinearity among covariates, retaining covariates with coefficients less than r = 0.7. I constructed one constant model, two models examining single detection covariates, two models testing single occupancy covariates, and eleven additive models for each species (16 EGS models and 16 SFS per season, Tables 6, 7 & 8). I ranked models with Akaike's information criterion (AIC) and adjusted SFS models to QAIC due to over dispersion ($\hat{c}_{2016} = 2.64$ and $\hat{c}_{2017} = 75.93$, Akaike 1973, Burnham and Anderson 2002).

Table 5. Covariates of Occupancy and Detection
Explanation of occupancy and detection covariates.

Covariate	**Description**
Occupancy	
Burn frequency (PF)	Average number of burns in a five-year period from 1992-2017
Canopy Cover (CC)	Percent canopy cover
Detection	
Temperature (Temp)	Maximum daily temperature in °C, z-standardized
Precipitation (Precip)	Daily precipitation in centimeters, z-standardized

Table 6. Eastern Gray Squirrel Occupancy Models

Eastern gray squirrel occupancy models ranked according to AIC model selection. Supported models (ΔAIC < 2.0) indicated by *.

Model	AIC	ΔAIC	ω_i	Likelihood	k	Deviance
ψ(PF+CC),γ(.),ε(.),p(Temp)*	203.34	0.00	0.9594	1.0000	7	189.34
ψ(PF),γ(.),ε(.),p(Temp)	210.92	7.58	0.0217	0.0226	6	198.92
ψ(PF),γ(.),ε(.),p(Temp+Precip)	212.85	9.51	0.0083	0.0086	7	198.85
ψ(PF+CC),γ(.),ε(.),p(Temp+Precip)	213.98	10.64	0.0047	0.0049	8	197.98
ψ(CC),γ(.),ε(.),p(Temp)	216.42	13.08	0.0014	0.0014	6	204.42
ψ(PF),γ(.),ε(.),p(.)	216.64	13.3	0.0012	0.0013	5	206.64
ψ(.),γ(.),ε(.),p(Temp)	217.44	14.1	0.0008	0.0009	5	207.44
ψ(PF+CC),γ(.),ε(.),p(.)	217.77	14.43	0.0007	0.0007	6	205.77
ψ(CC),γ(.),ε(.),p(Temp+Precip)	218.36	15.02	0.0005	0.0005	7	204.36
ψ(PF),γ(.),ε(.),p(Precip)	218.41	15.07	0.0005	0.0005	6	206.41
ψ(.),γ(.),ε(.),p(Temp+Precip)	219.38	16.04	0.0003	0.0003	6	207.38
ψ(PF+CC),γ(.),ε(.),p(Precip)	219.54	16.2	0.0003	0.0003	7	205.54
ψ(CC),γ(.),ε(.),p(.)	222.14	18.8	0.0001	0.0001	5	212.14
ψ(.),γ(.),ε(.),p(.)	223.19	19.85	0.0000	0.0000	4	215.19
ψ(CC),γ(.),ε(.),p(Precip)	223.92	20.58	0.0000	0.0000	6	211.92
ψ(.),γ(.),ε(.),p(Precip)	224.96	21.62	0.0000	0.0000	5	214.96

Table 7. Southern Fox Squirrel 2016 Occupancy Models
Southern fox squirrel occupancy models ranked according to QAIC model selection. Supported models (ΔQAIC < 2.0) indicated by *.

Model	QAIC	ΔQAIC	ω_i	Likelihood	k	Deviance
ψ(.),p(.)*	40.67	0	0.2523	1	2	96.68
ψ(.),p(Temp)*	42.26	1.59	0.1139	0.4516	3	95.59
ψ(PF),p(.)*	42.48	1.81	0.1021	0.4045	3	96.18
ψ(.),p(Precip)*	42.55	1.88	0.0985	0.3906	3	96.34
ψ(CC),p(.)*	42.58	1.91	0.0971	0.3848	3	96.43
ψ(PF),p(Temp)	44.07	3.4	0.0461	0.1827	4	95.09
ψ(.),p(Temp+Precip)	44.12	3.45	0.0449	0.1782	4	95.23
ψ(CC),p(Temp)	44.17	3.5	0.0438	0.1738	4	95.34
ψ(PF+CC),p(.)	44.19	3.52	0.0434	0.172	4	95.41
ψ(PF),p(Precip)	44.36	3.69	0.0399	0.158	4	95.84
ψ(CC),p(Precip)	44.45	3.78	0.0381	0.1511	4	96.09
ψ(PF+CC),p(Temp)	45.78	5.11	0.0196	0.0777	5	94.32
ψ(PF),p(Temp+Precip)	45.93	5.26	0.0182	0.0721	5	94.72
ψ(CC),p(Temp+Precip)	46.03	5.36	0.0173	0.0686	5	94.98
ψ(PF+CC),p(Precip)	46.06	5.39	0.017	0.0675	5	95.06
ψ(PF+CC),p(Temp+Precip)	47.64	6.97	0.0077	0.0307	6	93.95

Table 8. Southern Fox Squirrel 2017 Occupancy Models
Southern fox squirrel occupancy models ranked according to QAIC model selection. Supported models (ΔQAIC < 2.0) indicated by *.

Model	QAIC	ΔQAIC	ω_i	Likelihood	k	Deviance
ψ(.),p(.)*	5.6	0	0.2819	1	2	121.42
ψ(CC),p(.)*	7.55	1.95	0.1063	0.3772	3	117.39
ψ(.),p(Precip)*	7.58	1.98	0.1047	0.3716	3	119.64
ψ(.),p(Temp)*	7.58	1.98	0.1047	0.3716	3	120.13
ψ(PF),p(.)*	7.59	1.99	0.1042	0.3697	3	120.46
ψ(CC),p(Precip)	9.52	3.92	0.0397	0.1409	4	115.62
ψ(CC),p(Temp)	9.53	3.93	0.0395	0.1402	4	116.1
ψ(PF+CC),p(.)	9.55	3.95	0.0391	0.1388	4	117.39
ψ(PF),p(Precip)	9.56	3.96	0.0389	0.1381	4	118.68
ψ(PF),p(Temp)	9.57	3.97	0.0387	0.1374	4	119.17
ψ(.),p(Temp+Precip)	9.57	3.97	0.0387	0.1374	4	119.55
ψ(PF+CC),p(Precip)	11.52	5.92	0.0146	0.0518	5	115.62
ψ(CC),p(Temp+Precip)	11.52	5.92	0.0146	0.0518	5	115.52
ψ(PF+CC),p(Temp)	11.53	5.93	0.0145	0.0516	5	116.1
ψ(PF),p(Temp+Precip)	11.56	5.96	0.0143	0.0508	5	118.59
ψ(PF+CC),p(Temp+Precip)	13.52	7.92	0.0054	0.0191	6	115.52

RESULTS

I identified 36 individual SFSs during the summer 2016 sampling season and 124 individual SFSs during the spring 2017 sampling season. I estimated 0.37 SFSs/ha in 2016, and 1.26 SFSs/ha in 2017. Activity overlap indicated that SFSs and EGSs had similar diel activity patterns, but EGSs were most active in early morning and late evening hours while SFSs were most active around midday (Dhat1 = 0.62, Figure 6).

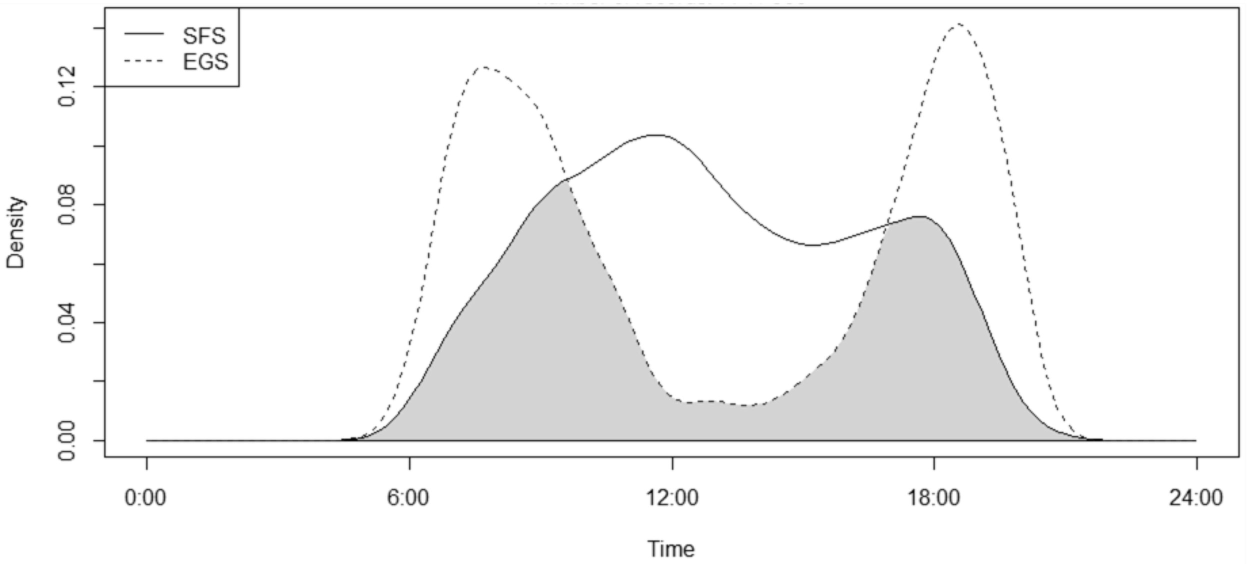

Figure 6. Southern Fox Squirrel and Eastern Gray Squirrel Activity Overlap
Kernel density estimate of eastern gray squirrel (EGS) and southern fox squirrel (SFS) activity throughout the day (0:00 – 24:00). Shaded area indicates activity overlap between species (Dhat1 = 0.62).

I tested for correlation among covariates of occupancy (r = -0.47) and detection (r = 0.19) and retained all covariates. Only one EGS occupancy model, ψ(PF+CC),γ(.),ε(.),p(Temp), was supported (ΔAIC < 2.0, Table 6). According to the supported model, average EGS occupancy was 0.45 ± 0.14 (95% CI: 0.21 – 0.69) and average detection probability was 0.72 ± 0.04 (95% CI: 0.64 – 0.80). The model failed to detect an association between canopy cover and occupancy (β = 2.98, SE = 3.29, Table 9), but occupancy was negatively associated with burn frequency (β = -1.751, SE = 0.864, Figure 7). Maximum daily temperature had a negative effect on detection probability (β = -0.278, SE = 0.039, Figure 8). Burn frequency and canopy cover were important occupancy covariates, accounting for 99.7% and 96.7% of model weights, respectively. Maximum daily temperature was the most important detection covariate, accounting for 99.7% of model weight. Daily precipitation was a poor predictor of detection probability and only accounted for 1.5% of model weight.

Table 9. Eastern Gray Squirrel Occupancy Beta Output
Beta output from supported eastern gray squirrel occupancy model, ψ(PF+CC),γ(.),ε(.),p(Temp). SE = standard error, LCL = lower 95% confidence limit, UCL = upper 95% confidence limit, significance denoted by *.

Parameter	β	SE	LCL	UCL
ψ	-3.02	2.93	-8.76	2.72
ψ.PF*	-1.75	0.86	-3.45	-0.06
ψ.CC	2.98	3.29	-3.48	9.43
γ	-0.56	0.63	-1.80	0.67
ε	-1.26	0.80	-2.83	0.32
P*	9.72	1.24	7.29	12.15
P.Temp*	-0.28	0.04	-0.35	-0.20

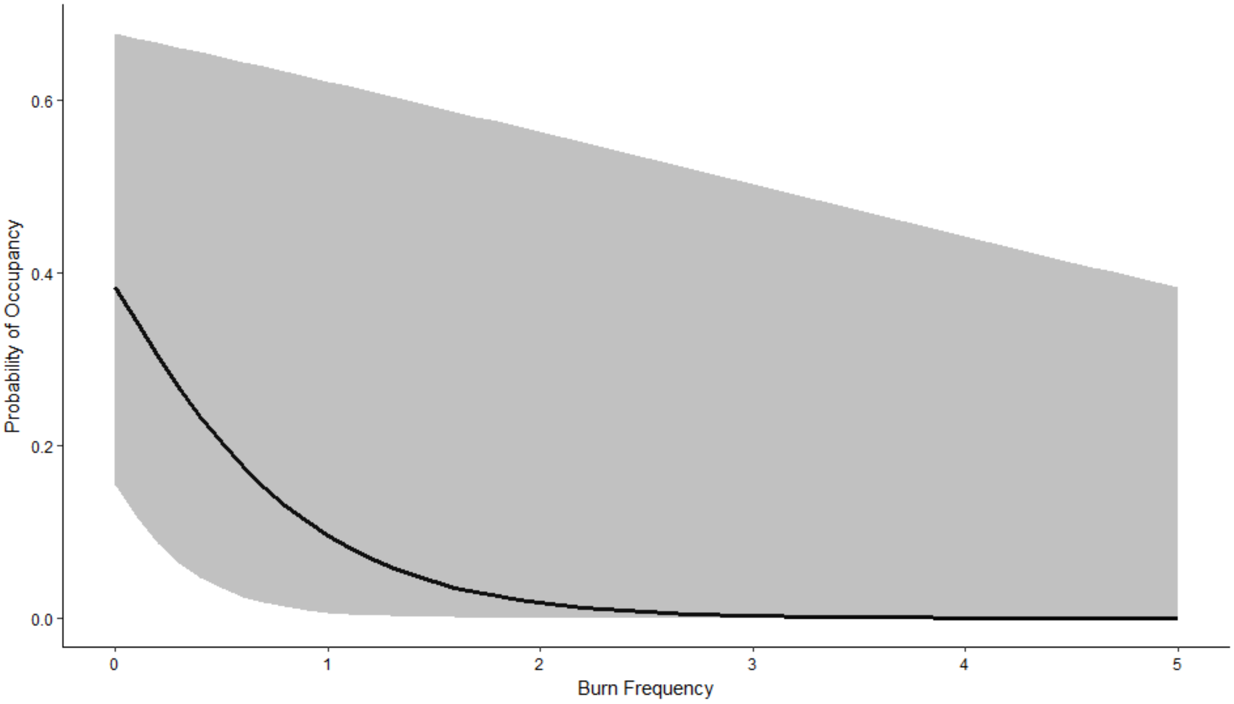

Figure 7. Effect of Burn Frequency on Eastern Gray Squirrel Occupancy
Relationship between burn frequency and eastern gray squirrel occupancy (ψ), based on output from ψ(PF), γ(.), ε(.), p(Temp).

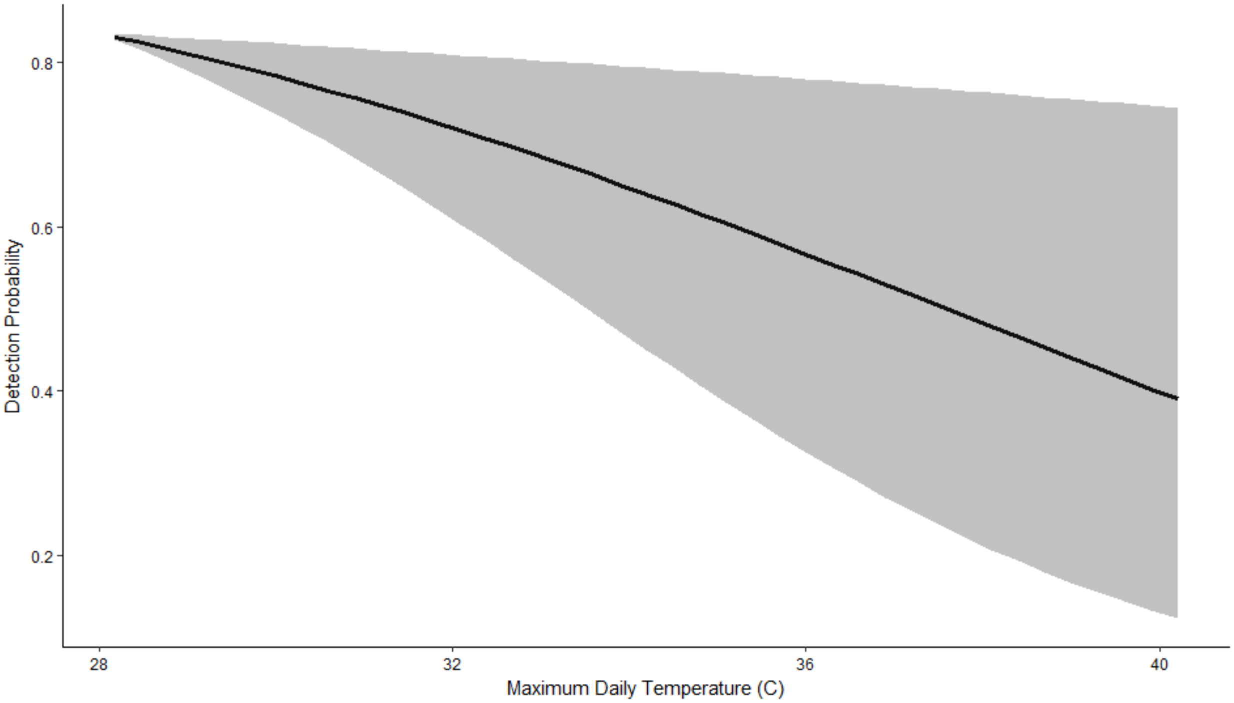

Figure 8. Effect of Maximum Daily Temperature on Eastern Gray Squirrel Detection Probability
Relationship between eastern gray squirrel detection probability (p) and maximum daily temperature, based on output from ψ(PF), γ(.), ε(.), p(Temp).

Five SFS occupancy models were supported for each season (ΔAIC < 2.0, Tables 7 & 8), but the constant model was most supported in each season, indicating poor overall model fit. Model-averaged SFS occupancy from the five supported models was 0.30 ± 0.08 (95% CI: 0.16 – 0.45) in 2016 and 0.51 ± 0.05 (95% CI: 0.35 – 0.57) in 2017. Model-averaged detection probability was 0.51 ± 0.04 (95% CI: 0.42 – 0.57) in 2016 and 0.50 ± 0.02 (95% CI: 0.45 – 0.54) in 2017. Six of the ten supported models included constant occupancy (Tables 7 & 8). Burn frequency was included in two supported models, but I failed to detect a significant association between burn frequency and SFS occupancy in either season (β_{2016} = -0.31, SE_{2016} = 0.44, β_{2017} = 0.68, SE_{2017} = 0.77, Tables 10 & 11). Likewise, canopy cover was included as an occupancy covariate in two supported models and indicated a significant, negative association in 2017, but I failed to detect a significant association between canopy cover and SFS occupancy in the first season (β_{2016} = -0.95, SE_{2016} = 1.91, β_{2017} = -19.32, SE_{2017} = 8.82, Tables 10 & 11, Figure 9). Six of the ten supported models included constant detection probability (Tables 7 & 8). Maximum daily temperature was included as a detection covariate in two of the ten supported models, but I failed to detect a significant association between maximum daily temperature and SFS detection probability in either season and the 2017 model was of poor fit (β_{2016} = -0.15, SE_{2016} = 0.08, β_{2017} = -0.16, Tables 10 & 11). Daily precipitation was included in two supported models, but I failed to detect a significant association between precipitation and SFS detection probability in either season (β_{2016} = 0.49, SE_{2016} = 0.84, β_{2017} = 6.77, SE_{2017} = 5.86, Tables 10 & 11). Burn frequency and canopy cover were important predictors of SFS occupancy based on parameter weights (29.4% and 28.4% in 2016, and 27% and 27.4% in 2017). Maximum daily temperature and daily precipitation were important predictors of SFS detection probability based on parameter weights (31.2% and 28.2% in 2016, and 27% and 27.1% in 2017).

Table 10. Southern Fox Squirrel 2016 Occupancy Beta Output
Beta output from supported SFS occupancy models. SE = standard error, LCL = lower 95% confidence limit, UCL = upper 95% confidence limit, significance denoted by *.

Model/Parameter	**β**	**SE**	**LCL**	**UCL**
ψ(.),p(.)				
ψ	-0.20	0.45	-1.08	0.68
P*	1.16	0.30	0.58	1.74
ψ(.), p(Temp)				
ψ	-0.20	0.45	-1.08	0.68
P*	6.34	2.81	0.84	11.85
P.Temp	-0.15	0.08	-0.32	0.01
ψ(PF),p(.)				
ψ	0.12	0.63	-1.13	1.36
ψ.PF	-0.31	0.44	-1.17	0.56
P*	1.16	0.30	0.58	1.74
ψ(.), p(Precip)				
ψ	-0.20	0.45	-1.08	0.68
P*	1.01	0.39	0.24	1.77
P.Precip	0.49	0.84	-1.16	2.13
ψ(CC),p(.)				
ψ	0.55	1.59	-2.56	3.67
ψ.CC	-0.95	1.91	-4.69	2.80
P*	1.16	0.30	0.58	1.74

Table 11. Southern Fox Squirrel 2017 Occupancy Beta Output
Beta output from supported SFS occupancy models. SE = standard error, LCL = lower 95% confidence limit, UCL = upper 95% confidence limit, significance denoted by *.

Model/Parameter	**β**	**SE**	**LCL**	**UCL**
ψ(.),p(.)				
ψ*	1.73	0.63	0.51	2.96
P*	1.66	0.25	1.17	2.15
ψ(CC),p(.)				
ψ*	19.68	8.52	2.98	36.37
ψ.CC*	-19.32	8.82	-36.61	-2.03
P*	1.66	0.25	1.17	2.15
ψ(.), p(Precip)				
ψ*	1.73	0.63	0.51	2.96
P*	1.52	0.27	0.99	2.04
P.Precip	6.77	5.86	-4.70	18.25
ψ(.), p(Temp)				
ψ*	1.73	0.63	0.51	2.96
P	6.29	--	--	--
P.Temp	-0.16	--	--	--
ψ(PF),p(.)				
ψ	1.19	0.79	-0.36	2.73
ψ.PF	0.68	0.77	-0.84	2.19
P*	1.66	0.25	1.17	2.15

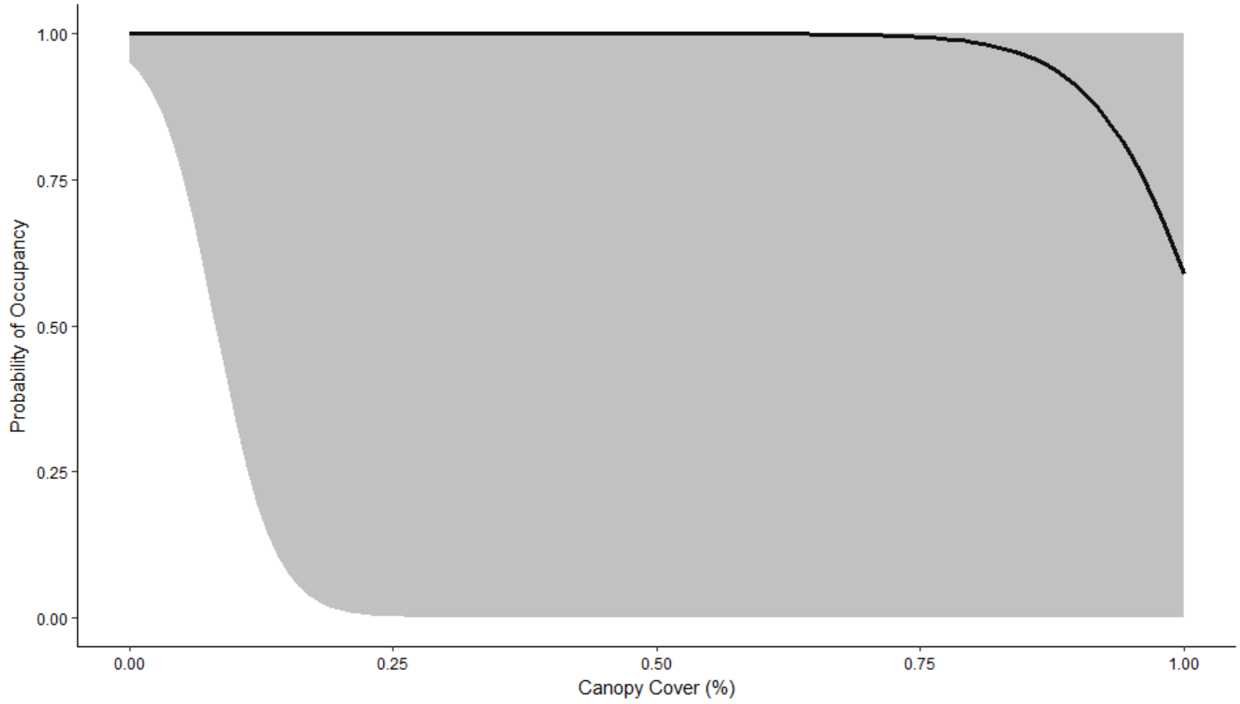

Figure 9. Effect of Canopy Cover on Southern Fox Squirrel Occupancy in 2017
Relationship between canopy cover and southern fox squirrel occupancy (ψ), based on output from ψ(CC), p(.).

DISCUSSION

Lee *et al*. (2008) reported 0.758 SFSs/ha on Spring Island in 1999. At that time, Spring Island SFS density was much higher than density estimates of other SFS populations, which ranged from 0.084 – 0.38 SFSs/ha (Hilliard 1979, Edwards *et al*. 1989, Weigl *et al*. 1989, Kantola and Humphrey 1990, Conner *et al.* 1999). I expected that Spring Island residents accurately perceived a decline in SFS populations due to anthropogenic development and the general trend of declining SFS populations (Wood and Davis 1981). I recorded 0.37 SFSs/ha and 1.26 SFSs/ha in June 2016 and April 2017, respectively. The difference in these estimates is likely associated with decreased activity of SFSs during summer months (Weigl *et al*. 1989), thus the spring 2017 density estimate is likely representative of the current Spring Island SFS population. Lee (1999) estimated density in May, and his estimate fell nearly halfway between my density estimates from April and June. Thus, the differences between our density estimates likely reflect decreasing SFS activity as temperature increases and food availability decreases. My hypothesis that Spring Island SFS density had declined since the 1990s was not supported, as SFS density appears to be similar to what Lee reported in 1999. Though my estimated SFS density (1.26 SFSs/ha) is high for the species, it is still much lower than densities achieved by many EGS populations (up to 15 EGSs/ha, Gurnell 1983).

However, habitat cues such as canopy cover and illumination influence behavior of prey species due to perceived predation risk (Thorson *et al*. 1992). Anthropogenic activity altered the habitat structure on Spring Island and may have affected the behavior of both SFSs and EGSs. In addition, citizen scientists and opportunistic data are often biased towards detections in frequently travelled areas, especially when searching for low-density populations such as SFSs (*e.g.,* roads, Fitzpatrick *et al*. 2009, Crall *et al.* 2010). Observations near homes with dense vegetation likely influenced perceived populations of SFSs on Spring Island.

I predicted that the shift in land use from managed quail plantation to nature preserve/residential community in the early 1990s altered the degree to which prescribed fire was used to manage wildlife habitat. I expected that this change allowed EGSs to disperse as habitat grew increasingly denser, increasing interactions between SFSs and EGSs. I observed both SFSs and EGSs at half of the sites sampled. Spring Island SFSs and EGSs had similar activity patterns, indicating they were not avoiding each other temporally (Figure 6), but EGSs did appear to be most active in early morning and late evening hours while SFSs were most active around midday.

Occupancy analysis indicated that EGSs were negatively associated with prescribed fire (Figure 7). Fire maintains an open understory and prevents woody stem encroachment within the longleaf pine ecosystem of the Southeast (Frost 1993), but EGSs prefer dense forests with woody undergrowth (Edwards *et al*. 1998). Southern fox squirrels prefer open, grassy understories (Edwards *et al*. 1998), but my SFS occupancy analysis failed to detect significant effects of burn frequency on occupancy. I did detect a significant, negative relationship between canopy cover and SFS occupancy (Figure 9), which is indicative of SFS preference for fire-maintained habitats (Boone *et al.* 2017). Occupancy analysis indicated that EGS detection probability is negatively associated with maximum daily temperature (Figure 8). Southern fox squirrel occupancy analysis suggested a negative relationship between maximum daily temperature and SFS detection probability, reflecting reduced activity during hot summer months when food was scarce (Weigl *et al.* 1989). On average, SFSs were less likely to occupy a site (0.40 ± 0.07) than EGSs (0.45 ± 0.14, Figure 10), and SFSs were less likely to be detected (0.50 ± 0.03) than EGSs (0.72 ± 0.04, Figure 11).

Spring Island, South Carolina still supports a high-density population of SFSs. Exurbanization influences habitat structure, particularly near heavily trafficked areas. The perceived decline in SFS population on Spring Island is likely due to the dense vegetation surrounding and hiding houses and observations biased towards areas with high human activity. Southern fox squirrels are found in comparatively low densities in more open areas that are managed with fire. In contrast, EGSs are found in higher densities in denser vegetation not managed with fire. Southern fox squirrels also have a lower detection probability than EGSs, potentially biasing population perceptions. In addition, high temperatures in summer months lead to periods of reduced activity in both species, and thus reduced detection. Residential communities striving to maintain natural diversity should preserve and manage habitat for specialists that struggle to integrate in humanized landscapes. Prescribed fire should be used to maintain suitable SFS habitat and provide ample opportunity for niche partitioning between SFSs and EGSs.

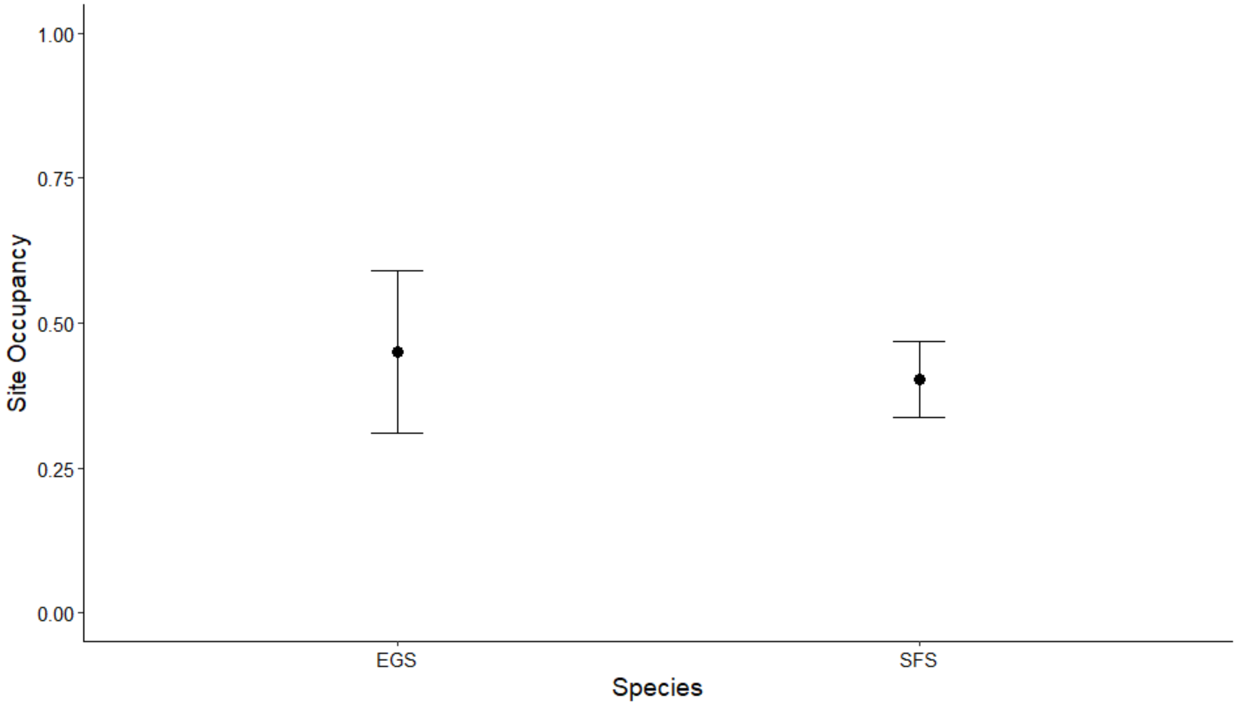

Figure 10. Comparison of eastern gray squirrel and southern fox squirrel site occupancy
Probability of occupancy by eastern gray squirrels (EGS) and southern fox squirrels (SFS) on Spring Island, South Carolina.

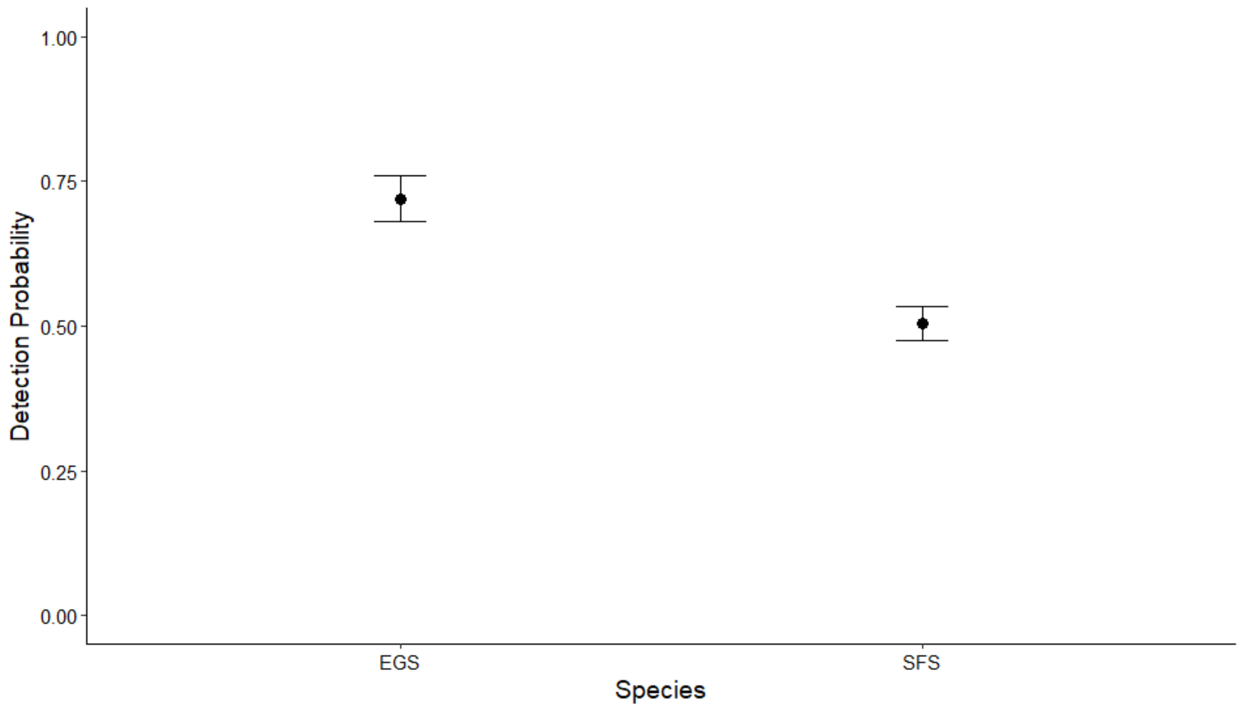

Figure 11. Comparison of eastern gray squirrel and southern fox squirrel detection probability
Eastern gray squirrel (EGS) and southern fox squirrel (SFS) detection probability on Spring Island, South Carolina.

CHAPTER 3

COMPARING SYMPATRIC SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) AND EASTERN GRAY SQUIRREL (*S. CAROLINENSIS*) FORAGING BEHAVIORS

INTRODUCTION

Cross-scale processes (*e.g.,* trophic cascades, keystone processes) are often characterized by emergent effects that propagate through ecosystems, fundamentally altering ecological structures and landscape dynamics. Top-down trophic effects extend beyond mortality due to predation and include an array of sublethal predator-prey interactions that cause behavioral changes and affect prey distributions (Thorson *et al.* 1992). Higher level predators create trophic cascades by changing prey densities and behaviors (Ripple *et al.* 2015). Consequently, changes in prey distributions cause alternating, inverse effects in lower trophic levels, cascading top-down through an ecosystem (Morgan *et al*. 2017).

Fire is a keystone process when evolutionary linkages between fire and vegetation create feedbacks that propagate fire regimes, allowing persistent open-canopy habitats (*e.g.,* subtropical savannas) to exist where climate and soils favor successional trajectories that result in closed canopy forests (Fill *et al.* 2012). The longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States is maintained by fire and characterized by an open canopy and sparse understory. Human activity and fire exclusion have reduced the ecosystem to 3% of its original range (Frost 1993). Closed canopy pine-hardwood forests replaced much of the area once dominated by the open canopy longleaf pine savanna (Frost 1993), a detrimental trend for the rare plant and animal populations tied to the fire-maintained, open canopy habitats (Sorrie and Weakley 2006). Habitat features such as canopy closure, illumination, and substrate influence risk perception and behavior of potential prey species (Thorson *et al.* 1992).

Southern fox squirrels (*Sciurus niger niger*, SFS) are habitat specialists associated with pine savannas and woodlands of the southeastern United States that have experienced population declines throughout their range due to habitat loss and fragmentation (Weigl *et al*. 1989, Perkins and Conner 2004). Southern fox squirrel life history strategies could contribute to the species' inability to rebound from population declines. Southern fox squirrels are one of the largest and most ground dwelling of all North American tree squirrels (Weigl *et al.* 1989). They are relatively long-lived (longevity ~ 7-10 years) and typically have just one litter per year with an average 2.5 pups, which suggests they are a k-selected species (Weigl *et al*. 1989, Tappe and Guynn 1998). Additionally, SFSs are normally found in low densities (average 0.05-0.35 squirrels/hectare, Weigl *et al*. 1989).

Eastern gray squirrels (*Sciurus carolinensis*, EGS) are habitat generalists found in dense forests with woody groundcover throughout the eastern United States (Brown and Batzli 1984). They typically live 8-9 years and frequently have two litters per year with an average 2.6 pups per litter (Barkalow *et al*. 1970). In addition, EGSs are often very abundant and reach high densities of up to 15 squirrels per hectare (Gurnell 1983).

Southern fox squirrels and EGSs are sympatric throughout the entirety of the SFS range. The species share similar food preferences (Smith and Follmer 1972, Edwards *et al.* 1998) and nest sites (Weigl *et al*. 1989, Edwards and Guynn 1995). Southern fox squirrel and eastern gray squirrel home ranges often overlap, and neither species is typically territorial, although aggressive behavior has been recorded in female fox squirrels during the breeding season (Armitage and Harris 1982, Brown and Batzli 1985a). Brown and Batzli (1985b) recorded evidence of competition between the species during field manipulations, and populations of fox squirrels have reportedly been replaced by EGS populations (Sexton 1990). Eastern gray squirrels may outcompete fox squirrels in areas with increased food availability and decreased density of predators (Van Der Merwe *et al.* 2005).

In the SE US, SFSs and EGSs limit competition through habitat partitioning (Weigl *et al.* 1989, Edwards *et al.* 1998), which is regulated by foraging behavior and behavioral responses to predators (Smith and Follmer 1972). However, fire suppression and human activity have reduced the longleaf pine ecosystem to 3% of its original range, allowing mixed pine hardwood forests to establish in areas once dominated by fire-maintained savanna-woodlands (Frost 1993).

In this study, I examined foraging and vigilance behaviors of sympatric SFSs and EGSs. I hypothesized that successional changes associated with fire exclusion homogenized landscape structures, altering risk perception and available foraging habitat for EGSs, therefore reducing opportunities for habitat partitioning and increasing interactions between shrinking remnant populations of SFS and expanding populations of EGSs. I used feed depots and time lapse videography to record squirrel foraging activity across a range of canopy closures to examine differences between the sympatric species. I hypothesized that the strength of sub-lethal predator effects would reflect historical habitat associations, and that SFSs and EGSs would respond differently to the increased risk of avian predation in open canopy habitats.

METHODS

STUDY AREAS

I recorded squirrel foraging activity on three properties in the southern South Carolina Coastal Plain. Each property had established populations of SFSs and EGSs and the preferred habitat types associated with each species. One study site was a privately-owned property within the Ashepoo, Combahee and Edisto (ACE) River Basin in Colleton County, SC. It was a 4,600-hectare plantation that consisted of a mosaic of upland pine savannas and woodlands, mixed pine hardwood forests, and hardwood lowlands. The uplands were managed for wildlife using timber harvests and frequent prescribed fires.

James C. Webb Wildlife Center and Management Area was a state-owned property in Hampton County, SC. It comprised 4,900 hectares that were a mixture of fields, upland pine savannas and woodlands, mixed pine hardwood forests, and hardwood bottoms. Frequent prescribed fires were used to maintain pine savannas and woodlands for wildlife habitat.

Nemours Plantation was a privately-owned property managed by the Nemours Wildlife Foundation within the ACE River Basin in Beaufort County, SC. It was a 4,000-hectare property of mixed pine hardwood forests, hardwood bottoms, and active pine savanna/woodland restoration areas. Timber harvests, longleaf pine plantings, and frequent prescribed fires were used to manage and restore pine savannas and woodlands on the property.

DATA COLLECTION

I established 20 random sites on each property. I built 1.5 x 0.9 m cypress feed depot frames with hardware cloth across the bottom. Between May and October 2016, I filled feed depots with a combination of 170 L of matrix (mini pine bark nuggets) and 14.2 L of bait (corn and pecans) and deployed one at each random site for five days with a Brinno TLC200 PRO HDR time lapse camera (Brinno Inc., Taipei City, Taiwan). I mixed bait into an unpalatable (*i.e.,* mini pine bark nugget) matrix to facilitate foraging activity. I set cameras to take a picture every three seconds from 6:00-21:00, and to compile photos into .AVI video files. I watched feed depot videos and recorded property, site number, species, duration, number of photos with head up, and number of photos with head down for each squirrel foraging event. I associated head-up posture with vigilance and head-down posture with foraging (Makowska and Kramer 2007).

STATISTICAL ANALYSIS

I calculated the percent time spent in a vigilant (head up) posture for each foraging event. I tested for differences in squirrel foraging event duration and vigilance by species with generalized linear mixed models using package lme4 (Bates *et al.* 2018) in Program R (R Core Team 2018). I treated site as a random effect because foraging events at the same site were not independent.

RESULTS

I recorded 166 squirrel foraging events, 61 were SFSs and 105 were EGSs. Southern fox squirrel foraging events were recorded at nine cameras, and EGS foraging events were recorded at six cameras. Southern fox squirrel foraging events ranged in duration from 6 to 3,261 seconds and averaged 464 seconds (SE = 81). Eastern gray squirrel foraging events ranged in duration from 9 seconds to 774 seconds and averaged 127 seconds (SE = 13). Southern fox squirrel foraging events lasted significantly longer than EGS foraging events (z = -3.47, p = 0.000515, Figure 12). Southern fox squirrel vigilance behavior ranged from 0 to 92% of the foraging session (SE = 3.1%). Eastern gray squirrel vigilance behavior ranged from 0 to 92% of the foraging session (SE = 2%). On average, SFSs spent 61% of the foraging event in a vigilant posture, which was significantly greater than the average 26% vigilance recorded for EGSs (z = 7.02, p = 2.24 e -12, Figure 13).

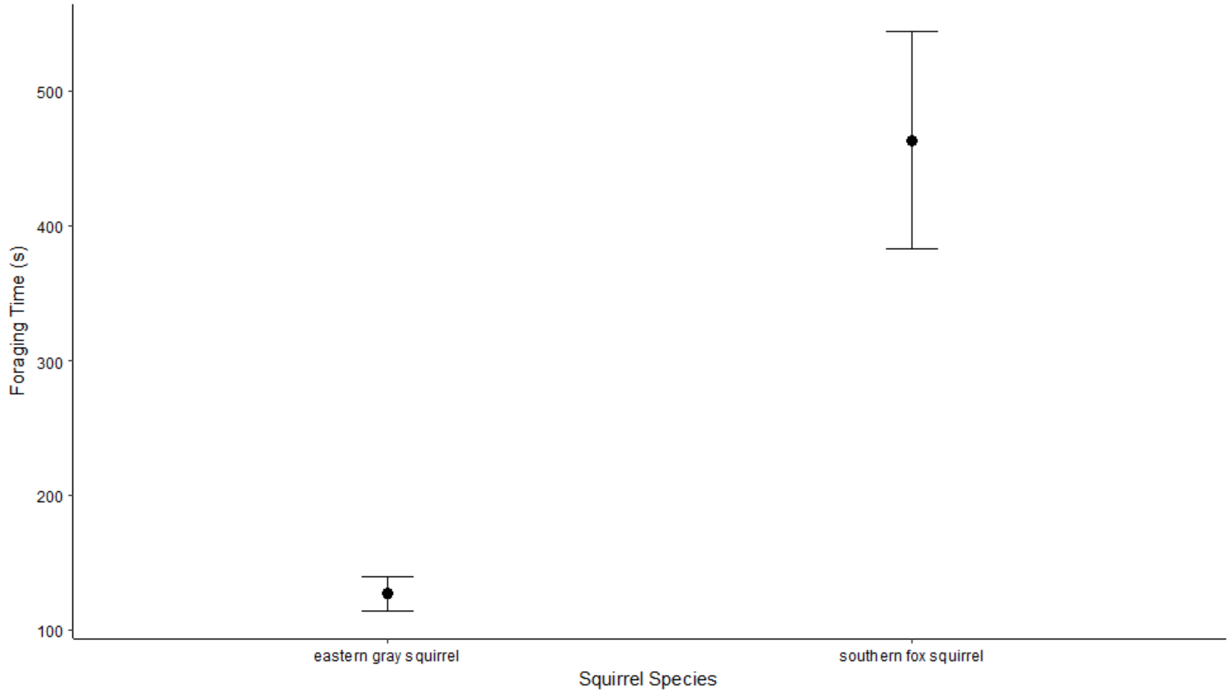

Figure 12. Squirrel Foraging Event Duration
Average duration of southern fox squirrel and eastern gray squirrel foraging events.

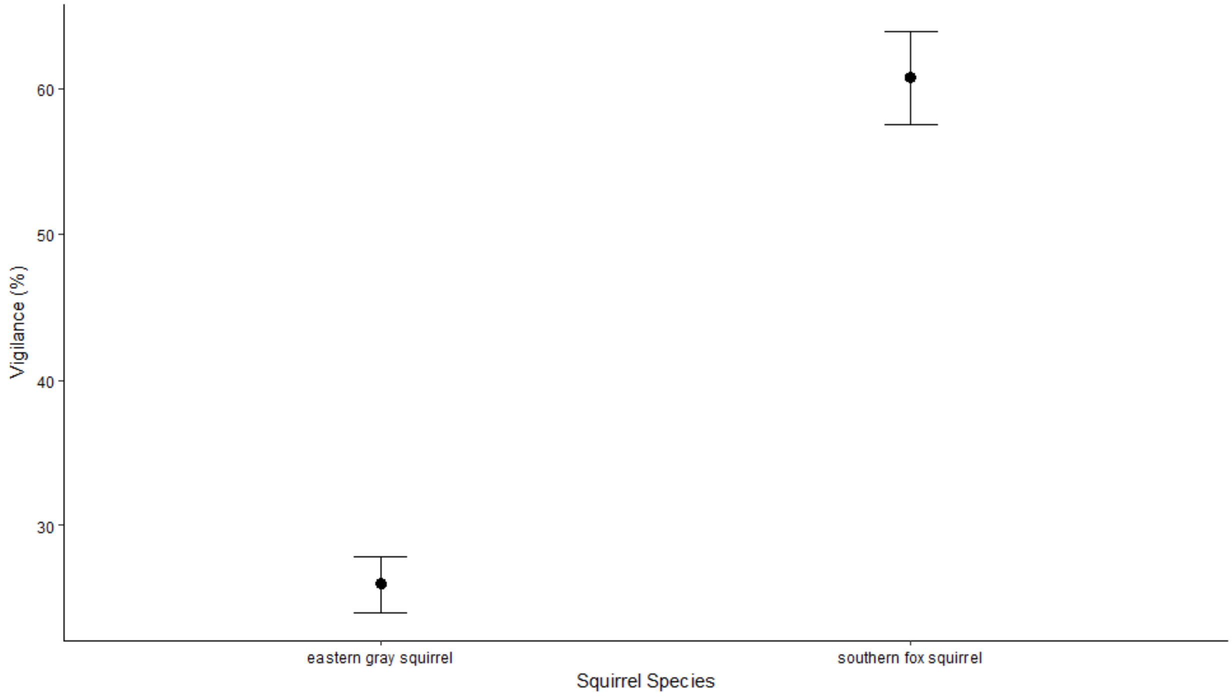

Figure 13. Squirrel Vigilance Behavior
Percent vigilance during eastern gray squirrel and southern fox squirrel foraging events.

DISCUSSION

Animals balance their need for food and fear of predators by varying the proportion of time they forage and are vigilant (Brown 1999). When perceived risk is high, individuals can increase vigilance or rate of food intake to increase safety from predators (Newman *et al.* 1988, Brown 1999). Perceived risk and its effects on foraging and vigilance behaviors can influence habitat selection (Gilliam and Fraser 1987) and the distribution of competitors across a landscape (Newman and Caraco 1987), but perceived risk is influenced by prey species (Kotler 1992), time since exposure to a predator (Kotler 1992), and habitat features (*e.g.*, canopy cover and illumination, Thorson *et al.* 1992).

Southern fox squirrel foraging events averaged 464 seconds (roughly 8 minutes, Figure 12), and just over 60% of that time was spent in a vigilant posture (Figure 13). Eastern gray squirrel foraging events averaged 127 seconds (roughly 2 minutes, Figure 12), and 26% of that time was spent in a vigilant posture (Figure 13). Southern fox squirrels are significantly more vigilant than EGSs, which supports my hypothesis that foraging behaviors would reflect historical habitat associations. The open-canopy structure of pine savannas and woodlands preferred by SFSs offer limited cover from predators. The perceived risk of predation is high under open canopy, forcing SFSs to increase vigilance. Van Der Merwe *et al.* (2005) observed fox squirrels in areas with higher predator densities when compared to EGSs, indicating increased vigilance is a behavioral adaption to open-canopied habitats. In addition, increased awareness of predators through vigilance behavior likely offsets the cost of foraging in areas far from cover. Conversely, I observed limited EGS vigilance behavior. The high percentage of canopy cover and dense woody understory in the forested habitats EGSs are associated with provide ample cover from predators, therefore decreasing the vigilant behavior required by this species.

Southern fox squirrels spend long periods of time foraging on the ground (Weigl *et al.* 1989). The sparse canopy of pine savannas and woodlands require that SFSs travel long distances between trees to find forage, contributing to large SFS home-range size (Weigl *et al.* 1989). However, the average EGS foraging event duration was significantly less than the average SFS foraging event duration. Eastern gray squirrels prefer dense forests with high basal area (Edwards *et al*. 1998) that likely provide increased opportunity for foraging in a smaller area. The short foraging event duration paired with limited vigilance behavior in eastern gray squirrels suggests that they may mitigate perceived predation risk through increased rate of food intake during foraging sessions as compared to southern fox squirrels (Newman *et al*. 1988, Brown 1999). Eastern gray squirrels are also more likely to use cached food items, contributing to their foraging success (Brown and Batzli 1985a). Thus, EGSs are adapted to, and better suited for, foraging in dense pine hardwood forests that offer higher densities of food and provide increased cover from predators.

Southern fox squirrels are significantly more vigilant than EGSs. However, EGSs likely mitigate predation risk through increased rate of food intake during significantly shorter foraging sessions (Newman *et al.* 1988, Brown 1999). Eastern gray squirrels also have a faster life history strategy (*e.g.*, higher fecundity and densities) that could contribute to increased competition between expanding EGS populations and remnant SFS populations. Increased rate of food intake partnered with an increased ability to locate caches indicate that EGSs may outcompete SFSs for food as suitable open canopy habitat is lost and the species become syntopic (Sexton 1990, Van Der Merwe *et al.* 2005).

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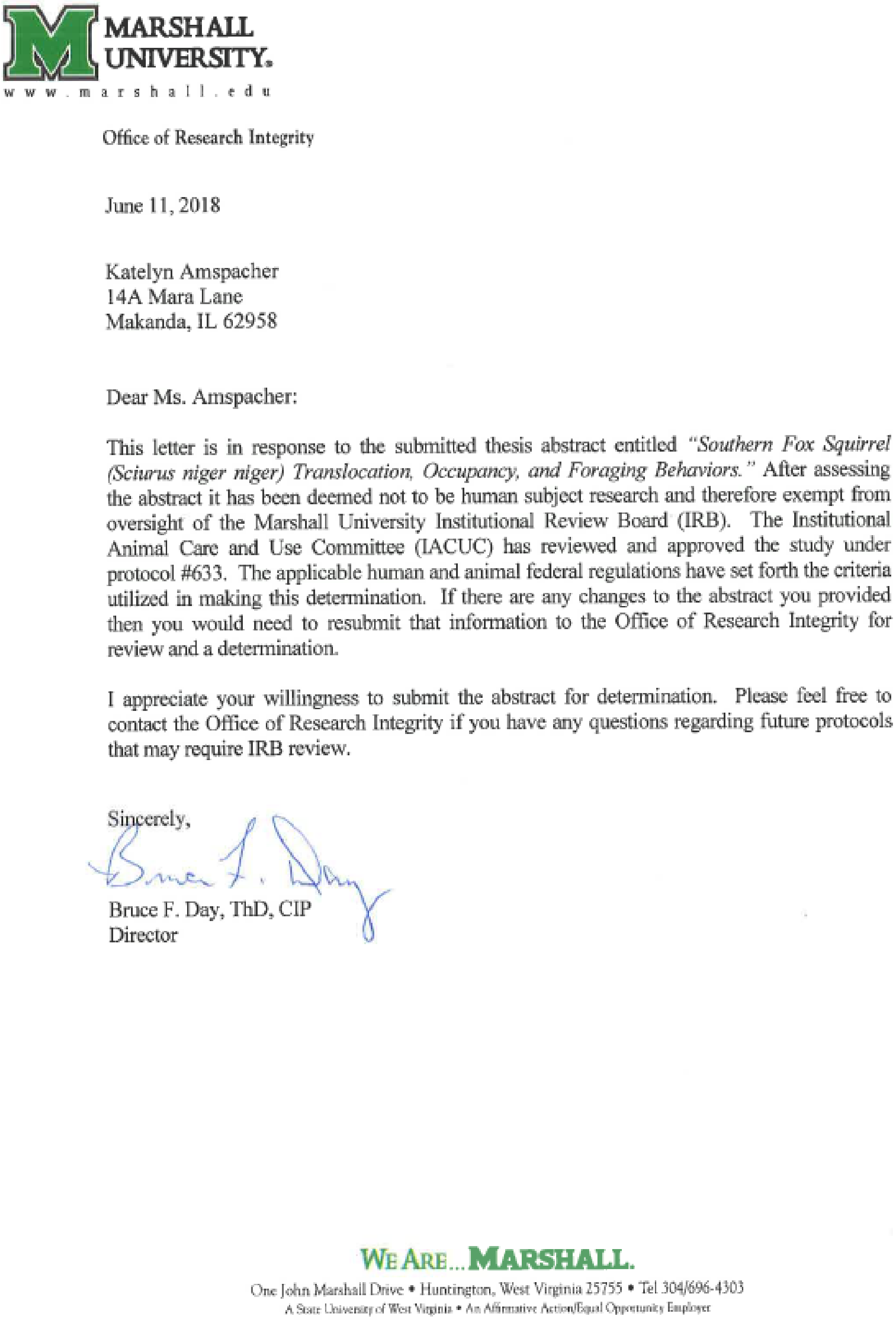
APPENDIX A: OFFICE OF RESEARCH INTEGRITY APPROVAL LETTER



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Office of Research Integrity

June 11, 2018

Katelyn Amspacher
14A Mara Lane
Makanda, IL 62958

Dear Ms. Amspacher:

This letter is in response to the submitted thesis abstract entitled *"Southern Fox Squirrel (Sciurus niger niger) Translocation, Occupancy, and Foraging Behaviors."* After assessing the abstract it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Institutional Animal Care and Use Committee (IACUC) has reviewed and approved the study under protocol #633. The applicable human and animal federal regulations have set forth the criteria utilized in making this determination. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day

Bruce F. Day, ThD, CIP
Director

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