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Southern fox squirrel (Sciurus niger niger) foraging behavior and population dynamics

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SOUTHERN FOX SQUIRREL (SCIURUS NIGER NIGER) FORAGING BEHAVIOR AND POPULATION DYNAMICS

A thesis submitted to
the Graduate College of
Marshall University
In partial fulfillment of
the requirements for the degree of
Master of Science
In
Biological Sciences
by
John Huang
Approved by
Dr. Shane Welch, Committee Chairperson
Dr. Jayme Waldron
Dr. Anne Axel

Marshall University
December 2020

APPROVAL OF THESIS

We, the faculty supervising the work of John Huang, affirm that the thesis, *Southern Fox Squirrel* (*Sciurus niger niger*) *Foraging Behavior and Population Dynamics*, 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.

Shane Welch 18 November 2020

Dr. Shane Welch, Department of Biological Sciences Committee Chairperson Date

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Dr. Anne Axel, Department of Biological Sciences Committee Member Date

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ABSTRACT

The change in the interaction between southern fox squirrel (*Sciurus niger niger*) and eastern gray squirrels (*Sciurus carolinensis*) provided an opportunity to examine sublethal effects of predation as it relates to a species' risk perception and habitat structure at two scales. The interactions allowed us to examine the evolutionary responses of the southern fox squirrel and eastern gray squirrel to predation risk reflective of their historically associated landscapes and habitat structures. Second, the succession of savanna woodlands into closed-canopy mixed forest provided an opportunity to assess the flexible behaviors of both species in response to changes in predation risks that occur with changes in current habitat structures (e.g., predation risks that vary within a patch). In this study, we quantified the foraging behavior and risk perception of the southern fox squirrel and eastern gray squirrel by compiling an ethogram from the camera footage obtained using a feed depot and a time-lapse camera. We expected southern fox squirrel vigilance behavior would have a positive relationship with change in canopy cover (i.e., vigilance behavior increases as canopy cover increases), whereas the vigilance behavior of the eastern gray squirrel would have an inverse relationship (i.e., vigilance behavior decreases as canopy cover increases). We expected southern fox squirrels would be more vigilant compared to the eastern gray squirrel. Contrary to our expectations, eastern gray squirrels spent a greater proportion of their foraging time being vigilant than southern fox squirrels. Our results were inconsistent with our predictions that vigilance behavior of southern fox squirrels would have a positive relationship with canopy cover, whereas eastern gray squirrels would have an inverse relationship with canopy cover. We failed to detect a significant effect of canopy cover on vigilance of southern fox squirrels and eastern gray squirrels. Our results suggest that eastern gray squirrels perceived greater risk from stationary and ambush predators, for whom vigilance

is an effective strategy to avoid predation, than active predators, while southern fox squirrels perceived greater risk from active predators, for whom vigilance is less effective in avoiding predation.

CHAPTER 1

EFFECTS OF CANOPY COVER ON FORAGING AND VIGILANCE BEHAVIOR OF SOUTHERN FOX SQUIRRELS AND EASTERN GRAY SQUIRRELS

Introduction

Foraging encompasses a range of actions related to a species' acquisition of food and thus foraging behaviors are key components of ecological and evolutionary feedbacks between species and their environment. (Ydenberg, Brown, & Stephens, 2007). Foraging behaviors are typically modeled as optimization problems where behaviors interact with environmental factors to maximize benefits while minimizing costs or risk (Brown, 1992; Brown, Morgan, & Dow, 1992). For many prey species foraging includes tradeoffs between active feeding and vigilant behaviors that reduce the risk of predation (Brown, 1988, 1992; Brown, Laundré, & Gurung, 1999; Brown, Morgan, et al., 1992; Laundré, Hernández, & Altendorf, 2001; Ripple, Larsen, Renkin, & Smith, 2001).

Top-down trophic effects extend beyond mortality due to predation, often influencing prey foraging behavior through sub-lethal effects of predation (Brown et al., 1999; Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017; Peers et al., 2018). Within a "landscape of fear" individuals must balance conflicting demands for food with safety when foraging and achieve this by allocating time towards vigilance while actively feeding (e.g., searching and handling) within a patch (Lima, 1998). Time allocation is a common measure of antipredator behavior and perceived risk, because it is directly related to resource acquisition rates, and by extension to prey fitness (Brown & Kotler, 2004; Brown et al., 1999; Laundré et al., 2001; Lima & Dill, 1990; Ripple et al., 2001). Fitness costs of anti-predatory behaviors include decreased food intake, lower body conditions (Dudeck, Clinchy, Allen, & Zanette, 2018), lower fecundity in females (Creel, Christianson, Liley, & Winnie, 2007; MacLeod, Krebs, Boonstra, & Sheriff, 2018; Zanette, White, Allen, & Clinchy, 2011), and reduced competitive ability in males (Lima, 1998). It is important to understand the role habitat structures and species interactions play in the foraging behavior of those who use them.

Microhabitat plays an important role as an indirect and reliable cue of predator risk, heavily influencing rodent foraging behavior (Bouskila, 1995; Bowers, Jefferson, & Kuebler, 1993; Brown, 1988; Brown, Morgan, et al., 1992; Kotler, Brown, & Hasson, 1991; Thorson, Morgan, Brown, & Norman, 1998). Habitat structures influence predatory risk and the prey's perception of risk either by allowing a prey to detect predators earlier, giving it a higher probability of escape if it is attacked, or by providing cover to reduce detection by predators (Lima, 1993). Prey species alter their foraging behavior in accordance with different structural elements, including presence of vegetation (Bowers et al., 1993; Brown, 1988; Kotler et al., 1991; Potash, Conner, & McCleery, 2019), diameter of vegetation (Lima, 1992), type of substrate (Brown, Arel, Abramsky, & Kotler, 1992), and illumination (Brown & Alkon, 1990; Hughes & Ward, 1993; Kotler, 1984).

The longleaf pine ecosystem is a diverse fire-dependent system noted for a high degree of endemism (Jackson, 1971; Noss et al., 2015; Tucker, Robinson, & Grand, 2004; Wall, Hoffmann, Wentworth, Gray, & Hohmann, 2012). Once a dominant ecosystem of the southeastern United States, now less than 3% remains (Frost, 1993). Many species dependent on the longleaf pine ecosystem are now relegated to isolated remnant patches (Frost, 1993; Greene & McCleery, 2017; Landers, Van Lear, & Boyer, 1995; Noss, 1989). Historically, the southeastern pine savannas and woodlands were shaped by recurrent fires that maintained open canopy savanna with a sparse understory (Greene & McCleery, 2017). Fire exclusion led to the loss of such habitat, as savannas and woodlands succeeded into closed-canopy mixed forest, a detrimental trend for the rare plant and animal populations tied to the fire-maintained, open canopy habitats.

Southern fox squirrels (*Sciurus niger niger*) are among the largest and most ground-dwelling of the North American tree squirrels, and a species of conservation concern due to population declines throughout their range (Weigl, Steele, Sherman, Ha, & Sharpe, 1989). Southern fox squirrels are important dispersal agents of hypogenous fungi, which have a mutualistic association with the roots of certain tree species such as that of the longleaf pine (Weigl et al., 1989). Southern fox squirrels are habitat specialists associated with pine savannas and woodlands (Perkins & Conner, 2004; Weigl et al., 1989). Conversely, eastern gray squirrels (*Sciurus carolinensis*) are habitat generalists associated with closed canopy forest (Brown & Batzli, 1984). Eastern gray squirrels use forested habitats but rely on similar resources as southern fox squirrels (e.g. food and nesting trees). Historically, interactions between eastern gray squirrels and southern fox squirrels were limited through habitat partitioning (Weigl et al., 1989). The change in the interaction between both species provides an opportunity to examine sublethal effects of predation as it relates to a species' risk perception and habitat structure at two scales. First the interactions allow us to examine the evolutionary responses of the southern fox squirrel and eastern gray squirrel to predation risk reflective of their historically associated landscapes and habitat structures. Second, the succession of savanna woodlands into closed-canopy mixed forest provides an opportunity to assess the flexible behaviors of both species in response to changes in predation risks that occur with changes in current habitat structures (e.g., predation risks that vary within a patch).

In this study, we used time-lapse videography and feed depots at the landscape-scale to examine the effects of canopy cover on the foraging behaviors of southern fox squirrels and eastern gray squirrels. We hypothesized that foraging behaviors under different degrees of canopy cover would reflect both historical habitat associations and microhabitat structures. Compared to eastern gray squirrels, fox squirrels have been observed in areas with higher predator densities, which indicates increased vigilance is a behavioral adaptation to open-canopied habitats (Amspacher, 2018; Van Der Merwe, Brown, & Jackson, 2005). We expected southern fox squirrels would be more vigilant compared to the eastern gray squirrel. The canopy structures of pine savannas and woodlands, preferred by southern fox squirrels, offer limited cover from aerial predators such as the red-tailed hawk, who primarily hunts in open canopy areas (Preston, 1990). Animals that rely on concealment to avoid being detected by predators perceive lower risk with greater levels of cover while animals that rely on early predator detection and fleeing to refuge perceive lower risk with open habitats (Arenz & Leger, 1997; Lima & Dill, 1990). Preferences towards open canopy suggest that southern fox squirrels (Perkins & Conner, 2004; Weigl et al., 1989) rely on the latter strategy to avoid predation, whereas based on the eastern gray squirrel’s preference with closed canopy structures (Edwards, Heckel, & Guynn Jr, 1998), eastern gray squirrels rely on the former strategy to avoid predation. We expected southern fox squirrel vigilance behavior would have a positive relationship with change in canopy cover (i.e., vigilance behavior increases as canopy cover increases), whereas the vigilance behavior of the eastern gray squirrel would have an inverse relationship (i.e., vigilance behavior decreases as canopy cover increases). This project provides insight into the role habitat structures play in the assessment of predation risk by southern fox squirrels and their interactions with eastern gray squirrels. It will also allow us to understand how fire prescription or fire exclusion might indirectly affect foraging behavior of the southern fox squirrel.

Method

Study Area

Spring Island is a 1200 ha sea island located in Beaufort County, South Carolina. Spring Island soils are characterized as fine sand or fine sandy loam (U.S.D.A, 1980). It has a subtropical climate characterized by mild winters, and hot humid summers (Kovacik & Winberry, 2019). Approximately 1000 ha of the island consist of stands of various hardwoods, live oaks (Q. Virginiana), pines (Pinus spp.), or mixed hardwood and pines (Lee, 1999). About 200 ha of the island are in fields, wildlife plantings, and a golf course (Lee, 1999). Frequent low-intensity prescribed fires were used to maintain large tracts of low-basal areas of pine and hardwood with an open, diverse understory. Such management practices provided habitat for other sensitive species including the red-cockaded woodpeckers (Picoides borealis), and southern fox squirrels (Moser, Jackson, Podrazsky, & Larsen, 2002; Prince, Chitwood, Lashley, DePerno, & Moorman, 2016) Spring Island was managed for quail from the mid-1900s until 1990, before it was sold for residential development. Development caused an increase in human activity and road construction creating a fragmented landscape and introduced a change in habitat structures (i.e. savannas and woodlands succeed into closed-canopy mixed forest). The Spring Island Trust, a nonprofit organization, was established to protect the environmental and cultural history and currently maintains 445 ha in nature preserves. Approximately 370 ha is managed using prescribed burns, and different 160 ha sections are burned annually.

Field Methods

Between 2 Aug 2019 and 16 Aug 2019, we established 12 random sites over a range of habitat types containing southern fox squirrels and/or eastern gray squirrels (Figure 1). At each site we set up a feed depot that consisted of a container (1.5 m x 1.5 m x 0.9 m; 2.025 m3) filled with a combination of 170 L of mini pine bark nuggets and 14.2 L of bait (pecans) to facilitate foraging. Feed depots were constructed using 1.5 x 0.9 m cypress frames with hardware cloth across the bottom. We used feed depots and time-lapse cameras to quantify foraging and vigilant behavior of southern fox squirrels and eastern gray squirrels. We visited each site every 2-3 days to restock bait and check cameras. Each feed depot was paired with a Brinno TLC200 Pro time-lapse camera (Brinno Inc., Taipei City, Taiwan) focused on the depot, set 70 cm above the ground and 1 m from the depot. Cameras were set to take a picture every 2 seconds from 5:00 – 21:00, and to automatically compile images into .AVI video format.

We quantified vegetation structure of sampling sites using modified techniques described by James and Shugart (1970). Within each site, five 0.04 ha circular plots were placed in randomly selected locations using randomly generated values for distance and azimuth away from the feed depot. We selected random distances between 20 m and 60 m based on radio-telemetry observations from a study population in Beaufort County, SC that indicated that squirrels move 20- 60 m weekly, and allowed us to assess the effects of canopy cover on squirrel foraging behavior at the patch-scale (J. Huang, personal observation). To measure percent canopy cover, we recorded 10 readings sighted using a densitometer along two 1-m wide and 10-m long transects. We recorded canopy cover every 2.8 m along perpendicular transects that were centered on the middle of each circular plot, totaling 20 readings per plot.

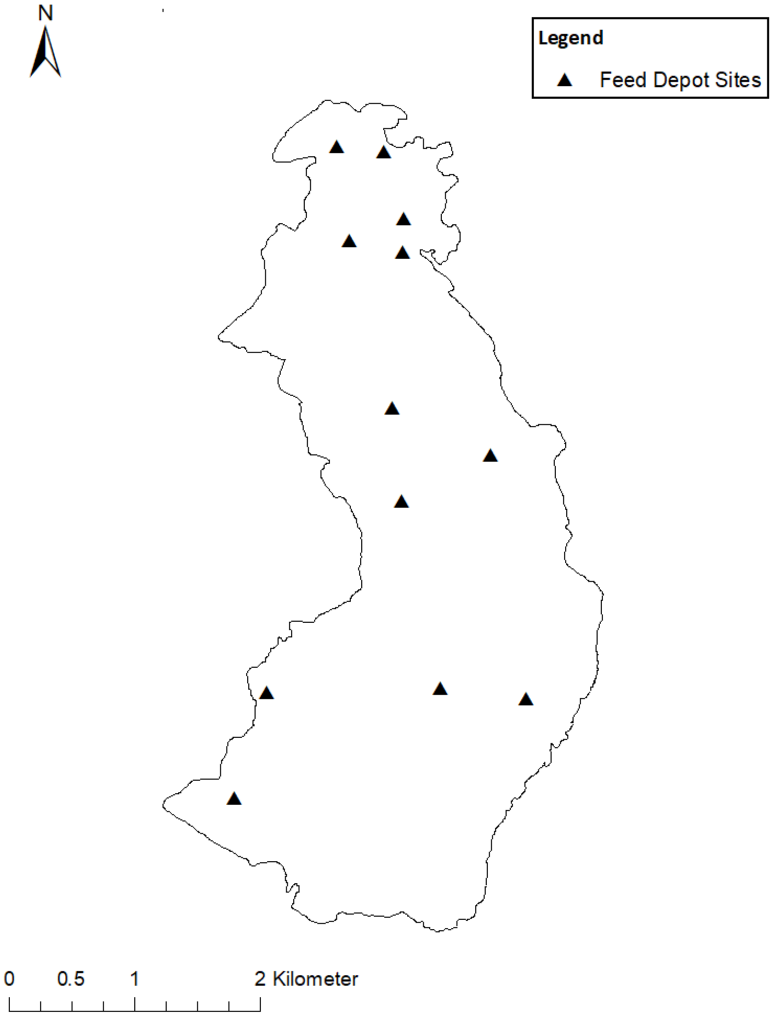

Figure 1. Feed Depot Sites
Locations of squirrel feed depot sampling sites on Spring Island, SC.

Ethogram

We quantified southern fox squirrel and eastern gray squirrel foraging behavior and risk perception by compiling an ethogram from camera footage. We classified behavior as searching when squirrels held their head down to the ground actively searching for food. We classified behavior as vigilant when squirrels held their head up scanning the surrounding area. We processed all camera footage using BORIS (Friard & Gamba, 2016), an event logging software for video/audio coding and live observations. We began timing the duration of a behavior when a squirrel entered the feed depot and stopped taking measurements when a squirrel left the feed depot. For each behavior, we summed the total amount of time (sec) squirrels displayed searching and vigilant behavior for each day. We then calculated the ratio of time allocated towards vigilance out of the total time a species spent foraging within a specific patch (i.e., total vigilance time / (total vigilance duration + total searching duration)). Time allocation between searching and vigilance is a common measure of antipredator behavior because it is directly related to resource acquisition rates and, by extension, to prey fitness (Brown & Kotler, 2004; Brown et al., 1999; Laundré et al., 2001; Lima & Dill, 1990; Ripple et al., 2001). This approach allowed us to quantify the trade-off between searching and vigilant behavior displayed under varying canopy cover.

Data Analysis

We used the ratio of time spent vigilant over total foraging time as our response variable. We ran an analysis of covariance (ANCOVA) to determine whether southern fox squirrels and eastern gray squirrels differ in the proportion of time spent vigilant over total foraging time, including canopy cover as a covariate. We treated site as a random effect to account for the lack of independence between observations from the same site. We examined residuals to test model assumptions. To meet normality assumptions, we transformed the response variables using an ordered quantile transformation (Peterson, 2017; Peterson & Cavanaugh, 2019). We examined the interaction term between canopy cover and species to test homogeneity of regression slopes, and non-significant ($p > 0.05$) interaction terms were removed. All analysis was conducted using package `nlme` in program R version 4.0.2 (R Development Core Team, 2020).

Results

I recorded 246 searching events, of which 91 were southern fox squirrels and 155 were eastern gray squirrels. I recorded 245 vigilance events, of which 90 were southern fox squirrels and 155 were eastern gray squirrels. On average, eastern gray squirrels allocated 0.83 ± 0.01 of foraging time being vigilant and southern fox squirrels allocated 0.76 ± 0.02 of foraging time being vigilant each day (Figure 2). The interaction term between canopy cover and species was not significant ($F_{1, 231}$ = 1.09, p = 0.30), indicating that canopy did not affect southern fox squirrels differently than eastern gray squirrels. After removing the interaction term, we detected a significant difference in allocation of time towards vigilance between species within a patch ($F_{1, 232}$ = 10.58, p = 0.001). Eastern gray squirrels allocated a greater proportion of their foraging time being vigilant compared to southern fox squirrels (Figure 2). We failed to detect a significant effect of canopy cover on vigilance ($F_{1,8}$ = 0.38, p = 0.56).

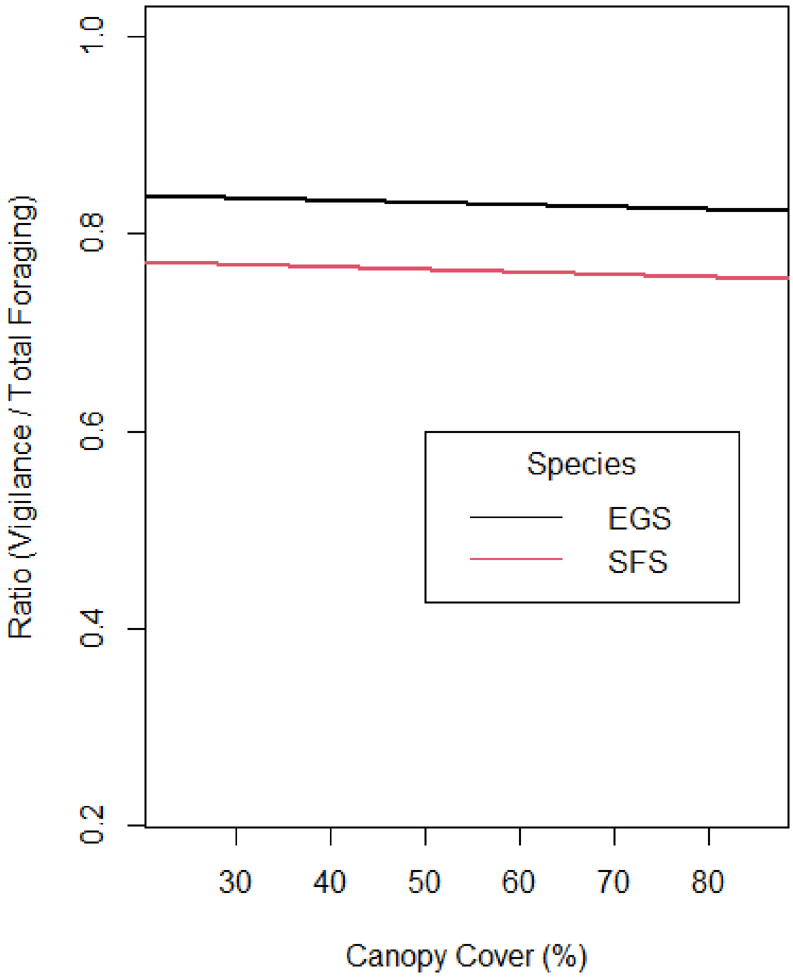

Figure 2. **Effects of canopy cover on the allocation of time towards vigilance**
Effects of canopy cover on the allocation of time towards vigilance for the southern fox squirrel and the eastern gray squirrel. The interaction term between canopy cover and species was not significant ($F_{1, 231} = 1.09$, $p = 0.30$), indicating that canopy did not affect southern fox squirrels differently than eastern gray squirrels. Eastern gray squirrels allocated a greater proportion of their foraging time being vigilant compared to southern fox squirrels ($F_{1, 232} = 10.58$, $p = 0.001$).

Discussion

Within a landscape of fear, animals must balance their needs for food and safety. To accomplish this, they allocate time between foraging and being vigilant (Steven L. Lima, 1998). Within this framework, prey respond to predators by becoming more vigilant or distancing themselves from suspected predators (Brown et al., 1999; Newman, Recer, Zwicker, & Caraco, 1988). When perceived risk is high, individuals increase vigilance and/or their rate of food intake to increase safety from predators (Brown et al., 1999; Newman et al., 1988). Our results suggest that in general eastern gray squirrels generally perceived higher predation risk compared to southern fox squirrels. Our results were inconsistent with our prediction that vigilance behavior of the southern fox squirrel would have a positive relationship with canopy cover, whereas eastern gray squirrels would have an inverse relationship with canopy cover. We failed to detect a significant effect of canopy cover on vigilance of southern fox squirrels and eastern gray squirrels.

Indirect cues of predatory risk can include any perceivable environmental factor that correlates with risk. In most habitats, there are areas of refuge and areas of higher predatory risk. Indirect cues of predation risk for active predators are less reliable than for stationary predators, (Preisser, Orrock, & Schmitz, 2007), which decreases the effectiveness of vigilance in reducing predation risk (Brown et al., 1999). Previous literature suggests that eastern gray squirrels were a common prey item of the sit-pursue predators such as red-tailed hawks (Koprowski, 2001) and Timber Rattlesnakes (*Crotalus horridus*), a terrestrial ambush predator (Goetz, Petersen, Rose, Kleopfer, & Savitzky, 2016). Predator-prey interactions are particularly affected by considerations for size (Thierry et al., 2011). Southern fox squirrels are nearly double the size of eastern gray squirrels. Eastern gray squirrels might perceive greater risk from stationary predators, where vigilance is an effective strategy to avoid predation, than active hunters. The body size of eastern gray squirrels may also make them more susceptible to stationary predators than southern fox squirrels. Southern fox squirrels might rely less on vigilance, because they perceive greater risk from active predators, for whom vigilance is less effective in detecting their presence.

Though we failed to detect an effect of canopy cover on vigilance of southern fox squirrels and eastern gray squirrels, this does not mean that canopy cover does not affect the allocation of vigilance by southern fox squirrels and eastern gray squirrels. The failure to detect an effect could be due to our short sampling period. Alternatively, there might be a temporal variation in perceived predation risk (Sperry, Peak, Cimprich, & Weatherhead, 2008). Future studies might examine predation risk across different seasons, and comparing perceived predation risk between multiple sites would provide us a better understanding of the relationship between habitat structures and nonlethal effects of predation.

As savannas and woodlands succeeded into closed-canopy mixed forest, habitats preferred by southern fox squirrels are lost while interaction with eastern gray squirrels increases (Sovie, Greene, & McCleery, 2020). Previous literature suggests that eastern gray squirrels may outcompete southern fox squirrels for food as suitable open canopy habitat is lost and the species become syntopic (Sexton, 1990; Van Der Merwe et al., 2005). Assessing species interactions and their relationship with environmental cues are important to understand wildlife conservation. Identifying such relationships could have implications for habitat management as well as furthering current understanding of the role those cues have in determining prey’s resource selection, antipredator behavior, and habitat requirements.

ABSTRACT

Conservation strategies for the southern fox squirrels have incorporated translocation efforts to augment and re-establish southern fox squirrel populations. Translocation has been used to successfully repatriate southern fox squirrel populations; however, none of these populations have been monitored long enough to examine recruitment and long-term survival. In our study we examined survival and recruitment of a repatriated population on the Marine Corp Recruit Depot – Parris Island (MCRDPI), South Carolina. Between January 2016 and July 2017, sixty-two southern fox squirrels were translocated onto MCRDPI, and were monitored using radio-telemetry and live-trapping efforts. We expected adult southern fox squirrel survival to be greater than juvenile southern fox squirrel survival. We also expected southern fox squirrel recruitment to be lower compared to other tree squirrel species. We used known fate models to estimate true survival probability. We modeled survival as a function of year, sex, season (to reflect differences in seasonal food abundance), stage (i.e., adult and juvenile), and squirrel mass. We used a Bayesian approach of the Jolly-Seber model as a restricted dynamic occupancy model to estimate recruitment. We failed to detect a difference between adult and juvenile southern fox squirrel survival. Only the survival model with year as a covariate was supported. Survival estimates were greatest in 2019 (0.73) and lowest in 2017 (0.23). Recruitment in 2016, 2017, and 2019 was 0.35, 0.43, and 0.22 respectively. Southern fox squirrel recruitment was low (0.22) compared to eastern gray squirrels (Sciurus carolinensis; 0.41), and high compared to red squirrels (Sciurus vulgaris;0.13). Our results indicated translocation as an efficient conservation tool for the long-term conservation of southern fox squirrels. Survival increased significantly after the two years post-translocation. Recruitment of our repatriated population was similar to

those of the Delmarva fox squirrel, whose successful delisting can be attributed to its many successful translocations.

CHAPTER 2

SURVIVAL AND RECRUITMENT RATES OF A REPATRIATED SOUTHERN FOX SQUIRREL (*SCIURUS NIGER NIGER*) POPULATION

Introduction

Life history theory provides a framework for conservation biologists to examine how specific population parameters (e.g., fecundity, recruitment, and survival) interact with environmental perturbations (e.g., habitat loss and fragmentation) to drive population declines that ultimately result in a specie's imperilment (Benton, Plaistow, & Coulson, 2006; Stearns, 1992). At the most basic level, only two values are needed to conclude the trajectory of a population. If the addition of individuals to a population by birth and immigration exceed the number of losses through emigration and death, a population is expected to increase. Should the relationships be reversed, the population is expected to decline (Rockwood, 2015).

Understanding the interactions of key population parameters and habitat loss and fragmentation are necessary to maximize conservation successes (Williams, 2013). For example, the population dynamics of a species characterized by a slow life history (i.e., low fecundity, delayed maturation, high adult survival) are often slow to show a positive response to habitat improvements (Williams, 2013). Because population responses of these species respond slowly to environmental change, they can persist at low densities in small isolated patches for extended periods of time and become vulnerable to population and environmental stochasticity.

Southern fox squirrels (*Sciurus niger niger*, henceforth SFS) are among the largest and most ground-dwelling of all the tree squirrels in North America (Weigl et al., 1989). The SFS is a habitat specialist tied to open-canopy habitats characteristic of the longleaf pine ecosystem (Perkins & Conner, 2004; Weigl et al., 1989). The longleaf pine ecosystem is a fire-dependent ecosystem noted for many rare plant and animal species (Jackson, 1971; Noss et al., 2015; Tucker et al., 2004; Wall et al., 2012). Less than 3% of this once dominant ecosystem of the southeastern United States, remains (Conner et al., 1999). Many LLE-dependent species, including SFS, are now relegated to small isolated remnant patches (Frost, 1993; Greene & McCleery, 2017; Landers et al., 1995; Noss, 1989). Southern fox squirrels have experienced range wide declines and are now a species of conservation concern.

Conservation strategies for the SFS have incorporated translocation efforts to augment and re-establish SFS populations. Translocation is an important conservation tool used to re-establish (i.e., repatriation) or augment populations in suitable habitat (Griffith, Scott, Carpenter, & Reed, 1989). Repatriation is a particularly important conservation tool because it can be used to increase the number of populations and help buffer the species from demographic and environmental stochasticity. Translocations have effectively been used to reintroduce Delmarva fox squirrels (*Sciurus niger cinereus*) to restored habitat (Bendel & Therres, 1994) leading to their delisting from the Endangered Species Act in 2015 (U.S. Fish and Wildlife Service Docket ID: FWS-R5-ES-2014-0021). Translocation has also been used to successfully repatriate SFS populations; however, none of these populations have been monitored long enough to examine recruitment and long-term survival (Dawson, Lee, Osborn, & Miller, 2009).

Detailed demographic data are needed to effectively manage and conserve SFS populations. For example, most SFS populations show an age structure biased toward adults (Weigl et al., 1989), suggesting differential survival among age classes. Birth rates are typically limited by a single spring breeding season and female fecundity and juvenile recruitment are low (e.g., births average 2.5 pups per female annually; (Weigl et al., 1989), with a 44-day gestation period and 90-days of dependency on the mother (Koprowski, 2001; Weigl et al., 1989). High adult survival and low reproductive output suggest that populations are likely sensitive to both demographic and environmental stochasticity.

Our objectives were to examine recruitment and survival of a repatriated SFS population. Southern fox squirrels are relatively long-lived, 7 – 10 years, and typically have one litter each year with an average of 2.5 pups, which suggests they are k-selected species, characterized by relatively high adult survival and producing few offspring. (Tappe & Guynn Jr, 1998; Weigl et al., 1989). We expected adult survival would be greater than juvenile survival because previous literature has suggested tree squirrel mortality is elevated during the first 3 to 4 months of life (Thompson, 1978). We expected recruitment would be low compared to other tree squirrel species because SFSs have fewer litters annually than other tree squirrel species. Effective conservation and management of SFS populations requires detailed demographic data. This study was important because it allowed us to gain a better understanding of the vital rates of SFSs.

Methods

Study Area

Marine Corps Recruit Depot – Parris Island (MCRDPI) is an active Marine Corps military base in South Carolina. The installation is located on a 3,220-ha sea island with approximately half of that acreage comprised of hard marsh. Marine Corps Recruit Depot 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.

Field Methods

Marine Corps Recruit Depot is within the historic range of SFS. Between January 2016 and June 2017, sixty-two SFS were captured at five donor sites in coastal South Carolina using Mosby-style wooden box traps baited with pecans (Amspacher, 2018; Day, Schemnitz, & Taber, 1980). Captured individuals were transferred to a wire and canvas handling cone to estimate reproductive maturity and determine sex. Lactating females were released immediately, allowing them to return to their nests. The squirrels selected for translocation were placed in covered wire Havahart traps (Woodstream Corp., Litiz, PA) and transported 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). Squirrels were allowed three hours for post-surgical recovery prior to release in a live oak (*Quercus virgiana*) grove on MCRDPI golf course (Amspacher, 2018). The release site was selected based on the prevalence of SFSs on golf courses in coastal South Carolina (Meehan & Jodice, 2010).

The repatriated SFS population was monitored post-translocation between January 2016 through December 2019 using Mosby-box traps (Day et al., 1980), and radio-telemetry. We baited Mosby-style wooden box traps with pecans and set them at the base of trees in close proximity to the SFS feeding remains. We transferred captured SFS to wire Havahart traps (Woodstream Corp., Litiz, PA) to determine sex and estimate reproductive maturity; all lactating females were released immediately. We transported individuals to Sea Island Animal Hospital (Lady's Island, SC) to be anesthetized with 20-30 mg of ketamine hydrochloride plus 1 mg acepromazine. We then fitted each SFS with a radio collar (Advanced Telemetry Systems, Inc., Isanti, MN, Model M1640, 6.5g; 642-day battery life) and a passive integrated transponder (PIT) tag. We used radio collars to monitor survival, while the PIT tags were used for identification during capture-recapture sessions. Both were used for identification, but PIT tags were more reliable and had a lower probability of tag loss. We measured mass and body-length from the head to the base of the tail, and photographed fur coloration patterns. We replaced radio collars for recaptured individuals with new ones. We examined captured females for any signs of pregnancy or previous instances of reproduction. Individuals were allowed to recover for 24 hours following anesthetization, providing them ample time to recover from the procedure, before a hard release at their point of capture. After the SFSs were released, we radio-located individuals twice weekly with a receiver (Advanced Telemetry Systems, Inc., R4000) and Yagi antenna. We recorded SFS locations using a Trimble Juno 3 GPS unit with a spatial accuracy of 2-5 m (Trimble Inc., Sunnyvale, CA).

Data Analysis

We estimated in-situ recruitment (b_t), number of individuals entering the population (B_t), mean capture probability(p), and superpopulation size (N_s) with capture-recapture data from 2016 – 2019 using a Bayesian approach of the Jolly-Seber model as a restricted dynamic occupancy Model (Kéry & Schaub, 2011; Royle & Dorazio, 2008). We excluded the year 2018 because only recaptures were recorded, precluding the ability to obtain estimates. In this approach, capture-recapture data were described as the result of the state process and observation process. The state process represents true, but unknown, ecological process, whereas the observation process describes imperfect observation of ecological processes in the data collected (Kéry & Schaub, 2011; Royle & Dorazio, 2008). The observation process is dependent on the state process, and the state process is estimated from the analysis. Within the restricted occupancy formulation of the Jolly-Seber model, individuals could be in three possible states:

not yet entered, alive, or dead. Ecological processes of entry and survival allow individuals to transition between these states. Individuals can enter and leave the population in an analogous way to occupancy models, where sites and patches are colonized and recolonized (Royle & Dorazio, 2008).

To consider individuals that were part of the population but not captured, we used data augmentation (Royle & Kéry, 2007). We added “pseudo-individuals” (n = 5) that were never captured, of which their capture history is all zeros. We determined the number of “pseudo-individuals” based on the minimum number of individuals thought to have been recruited into the population after the first year of translocation. Each female that survived until the following breeding season in the first year of translocation was assumed to have had at least one individual fledge from the nest. Using data augmentation, we introduced a latent variable that linked “pseudo-individuals” with the probability of being part of the study population. The model was fitted using JAGS 4.3.0 (Plummer, 2015) and R 3.5.2 (Team, 2014). The R packages used were “coda” (Plummer, Best, Cowles, & Vines, 2006) and “jagsUI” (Kellner, 2015). We ran 3 Markov Chains (MCMC), with 60,000 iterations, and discarded the first 30,000 as burn-in, thinning samples by 3 to result in 30,000 samples. The initial values of all the parameters were assigned by random functions, and we used vague priors’ distributions. We checked model convergence with the Gelman-Rubin statistic, and by visually inspecting plots of the chains (Brooks & Gelman, 1998).

The Jolly-Seber model assumes unmarked animals in the populations have the same probability of capture as marked animals in the population (i.e., newly captured unmarked animals are a random sample of all unmarked animals in the population). Animals must also retain their tags throughout the experiment, tags must be read properly, sampling periods are instantaneous, all emigration from the sampled area is permanent, and the fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

We estimated survival using radio-telemetry data within a known fate modeling framework in program MARK (Cooch, 2008; White & Burnham, 1999) version 9.x implemented through the RMark package (Laake, 2013) in program R version 4.0.2 (R Development Core Team, 2020). We formatted the encounter history files to include one live/dead entry per month for twelve months and created three entries for SFSs present on MCRDPI in 2016, 2017, and 2019. All months were assumed to have equal survival probabilities. We modeled survival as a function of year, sex, season (to reflect differences in seasonal food abundance), stage (i.e., adult and juvenile), and squirrel mass (z-standardized) (Table 2). We compared five candidate models and a constant survival model (Table 3) using Akaike's Information Criterion adjusted for small sample size (Burnham & Anderson, 2002), retaining models with $\Delta AIC_c < 2.0$ for inference. We modeled survival over three years (2016, 2017, 2019), and by season (Jan-Mar, Apr-June, July-Sept, Oct-Dec). These four seasons captured differences in seasonal food availability. From January through March, food resources were variable and beginning to decline (i.e., dependent on fall mass production and vary from year to year). From April through June, food resources are abundant. During July – September, limited food resources are available to the squirrels, and from October through December is potentially the best food period for the squirrels (e.g., acorns and hickory nuts).

Results

We marked 82 individuals over the four-year study. We marked 27 squirrels in 2016 and 35 individuals in 2017. Twenty-seven individuals in 2016 and 35 individuals in 2017 were marked during translocation, and 20 individuals marked were born on MCRDPI. Of the total number of individuals marked, 30 were juveniles and 52 were adults during first capture. Eleven individuals were recaptured during the study. In 2016 and 2017, 31 dead SFSs were recovered as a result of predation (n =22), vehicular strikes (n=1), and unknown causes (8) (Amspacher, 2018). In 2019, four squirrels were recovered and the cause of death was unknown. We also recovered 4 radio-collars that were dropped.

Recruitment and Abundance Estimates

There was no evidence for lack of convergence for the Jolly-Seber model, with the Gelman-Rubin statistic less than ≤1.02 for all monitored parameters. Mean capture probability was 0.83 (95% CRI:0.71 – 0.91) across 2016, 2017, and 2019. Annual recruitment rate was 0.35 (95% CRI: 0.24 – 0.46) in 2016, 0.43 (95% CRI: 0.32 – 0.55) in 2017 and 0.22 (95% CRI: 0.12 – 0.33) in 2019. Per-capita recruitment rate in 2017 was 0.81, and 0.55 in 2019 (Figure 3). Annual abundance varied throughout the study period (Table 1), with a mean estimated superpopulation size of 86 (95% CRI:84 – 87). The number of individuals that entered the population was estimated to be 29 (95% CRI: 26 – 34) in 2016, 37 (95% CRI: 33 – 43) in 2017, and was 19 (95% CRI: 14 -24) in 2019 (Figure 3).

Known Fate Survival Analysis

Only the survival model with year as a covariate received support (Table 3). Survival averaged 0.73 ± 0.09, 0.23 ± 0.06, and 0.42 ± 0.10 for 2019, 2017, and 2016, respectively (Table

4). Survival was higher in 2019 as compared to 2016 (Figure 4), while the survival rate in 2017 was less than 2016 (Figure 4).

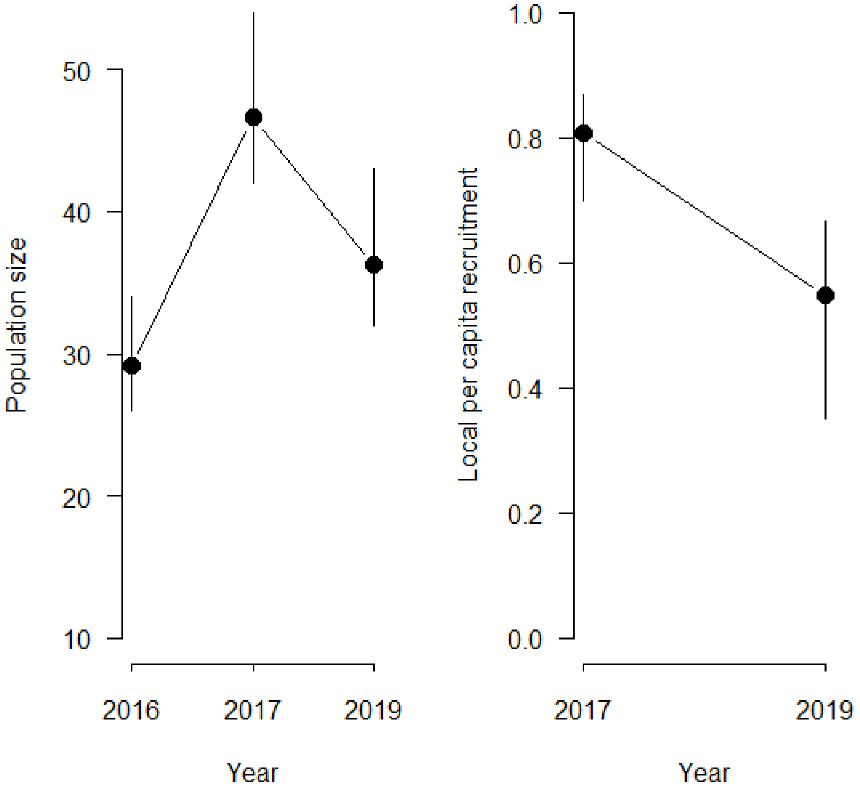

Figure 3. Southern fox squirrel population size and Local per-capita recruitment
Annual population size (Nt) for 2016, 2017, and 2019 (left). Populations increased from 2016 to 2017, as expected because squirrels were translocated onto MCRDPI. Population size decreased from 2017 through 2019. Per-capita recruitment rate (left) interpreted as the per capita number of southern fox squirrels produced in a breeding season that survived into the population into the next year. Per-capita recruitment rate was observed to have decreased from 2017 through 2019.

Table 1. Estimates from the Jolly-Seber model

Posterior means and 95% credible intervals (CRI) for parameters of interest under the restricted dynamic occupancy parameterization of the Jolly-Seber model for recruitment and abundance of the southern fox squirrel Sciurus niger niger in the MCRDPI, SC for 2016, 2017, and 2019 with uninformative priors where pmean is the mean capture probability from 2016 – 2019 (excluding 2018), Nt is the abundance estimate in year t, Nsuper is the total number of individuals that were ever a member of the population from 2016- 2019, bt is the in-situ recruitment rate estimate in year t, and Bt (individuals born and surviving 1 year) is the number of recruits in year t.

Parameter	**Mean**	**95% CRI**
p_{mean}	0.826	0.71 – 0.91
N_{2016}	29	26 - 34
N_{2017}	46	42 - 54
N_{2019}	36	32 - 42
N_{super}	86	84 – 87
b_{2016}	0.345	0.24 – 0.46
b_{2017}	0.433	0.32 – 0.55
b_{2019}	0.222	0.12 – 0.33
B_{2016}	29	26 – 34
B_{2017}	37	33 – 43
B_{2019}	19	14 -24

Table 2. Known Fate model Covariates
Description of the covariates used for the known fate models.

Covariate	Description
Year	Includes the years 2016, 2017, and 2019. Classified as a categorical variable
Sex	Individuals were identified as either male or female. Classified as a categorical variable
Mass	Mass of individuals when they were captured during a sampling period. Classified as a continuous variable.
Season	Seasonal variation based on food availability. Classified as a categorical variable.
Stage	Individuals were classified as adult or subadult during a sampling period. Classified as a categorical variable.

Table 3. Known fate models
Known fate survival models ranked according to AIC_c model selection. ΔAIC_C = the difference between the AIC_C value for the current model and the top supported model; K = number of model parameters. Models are listed in order of support.

Model	AICc	ΔAICc	Weights	Likelihood	K	-2log(L)
S(Year)	338.31	0	0.99	1.00	3	332.27
S(Season)	351.16	12.86	0.00	0.00	4	343.11
S(Sex)	351.51	13.20	0.00	0.00	2	347.49
S(.)	351.76	13.46	0.00	0.00	1	349.76
S(Mass)	352.08	13.77	0.00	0.00	2	348.06
S(Stage)	353.25	14.95	0.00	0.00	2	349.24

Table 4. Known Fate model with year as a covariate
Betas, standard error, and 95% confidence intervals for each year (2016, 2017, and 2019)

Year	β	SE	95% LCI	95% UCI
2016	2.59	0.29	2.03	3.15
2017	-0.56	0.35	-1.25	0.12
2019	1.05	0.48	0.11	1.99

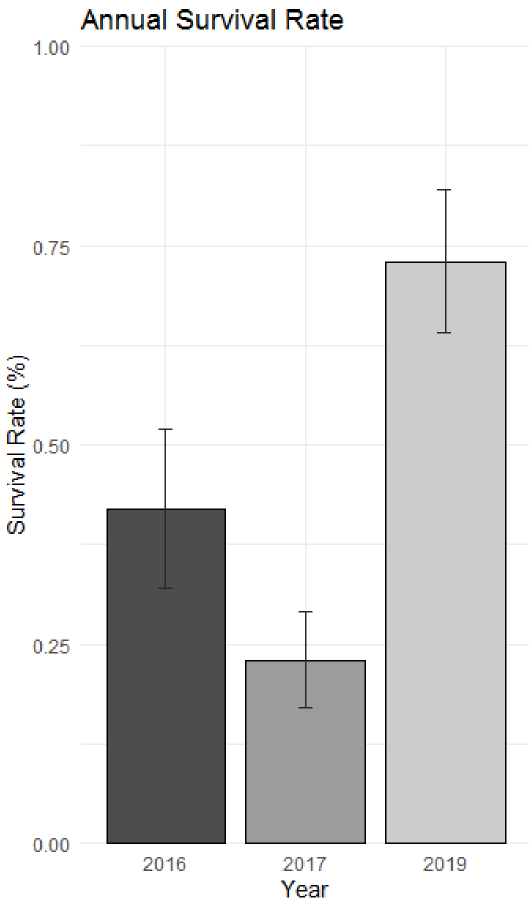

Figure 4. Comparison of survival rates between years
Annual survival rate estimated using a known fate model analysis. Southern fox squirrel survival rate was greater in 2019 compared to 2017 and 2016.

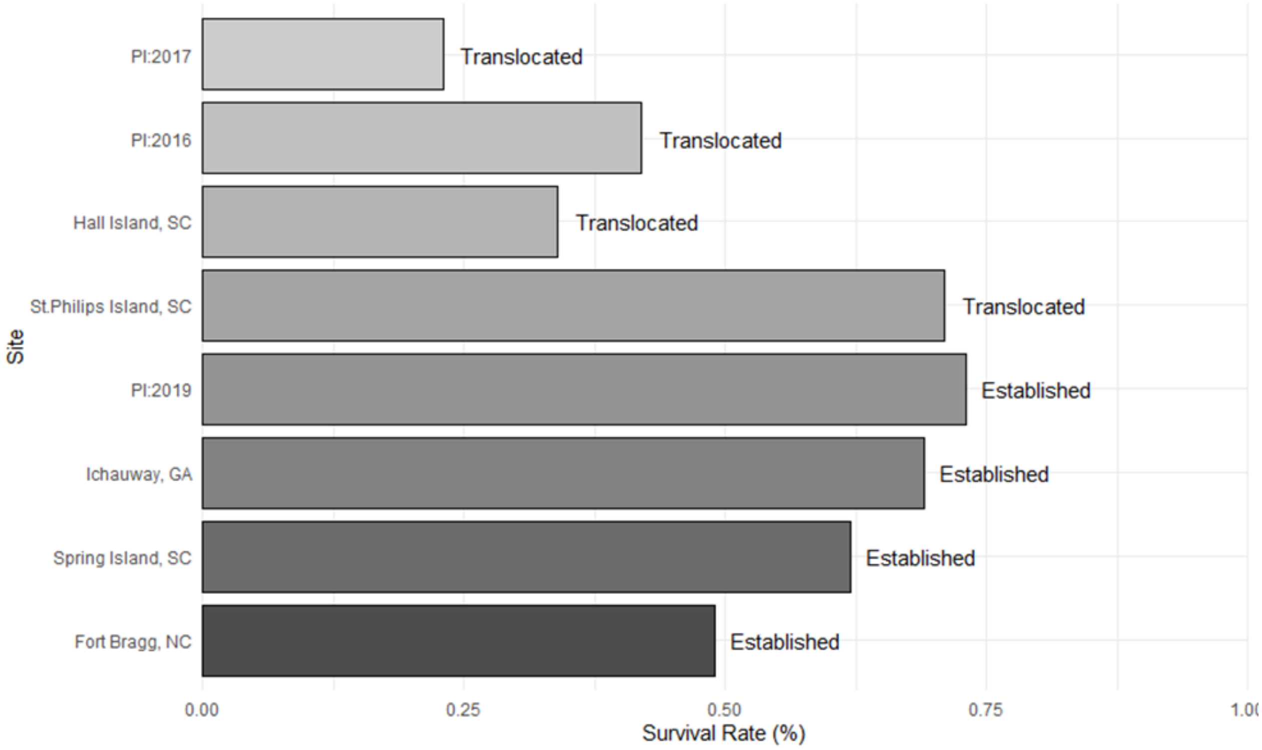

Figure 5. Comparing survival of repatriate southern fox squirrel population on MCRDPI and other translocated and established populations

Estimated survival rates from our study and from other studies of translocated and established southern fox squirrels' populations (Conner, 2001; Dawson et al., 2009; Lee, Osborn, & Miller, 2008; Prince & DePerno, 2014). The survival rate of our repatriated population in 2016 was greater than the translocated population study on Hall Island, SC (Dawson et al., 2009), but much lower than another conducted on St. Philips Island, SC (Dawson et al., 2009). The survival rate in 2017 was much lower than translocated population studies at other sites (Dawson et al., 2009). The survival rate in 2019 was greater than established population from other studies (Conner, 2001; Lee et al., 2008; Prince & DePerno, 2014).

Discussion

Southern fox squirrel recruitment was below 0.35 in 2016, 2017, and 2019. Recruitment was highest in 2016 and 2017, which was consistent with our expectation that recruitment estimates would be highest during translocation years. We suspect these estimates may have been artificially inflated due to translocation, but SFS may also exhibit density-dependent recruitment (i.e., as population size/density increases, per-capita recruitment decreases; (McConnell et al., 2018).

We hypothesized that SFSs would have slower life history compared to other squirrel species. Our estimates of SFS juvenile recruitment rates were lower than the rates estimated for red squirrels (*Sciurus vulgaris*) in two large conifer forests in northern England (Wauters, Lurz, & Gurnell, 2000). Wauters et al. (2000) examined juvenile recruitment rates for red squirrels at two sites, one consisting only of red squirrels, and another that had eastern gray squirrels (*Sciurus carolinensis*) and red squirrels. At sites with only red squirrels the recruitment rate was 0.5, while at sites with both eastern gray squirrels and red squirrels, red squirrel recruitment rate was 0.13 (Wauters et al., 2000). Eastern gray squirrel recruitment rate was 0.41 at sites with red squirrels (Wauters et al., 2000). In our study, the recruitment rate in 2019 was lower than red squirrels at sites with only red squirrels. The recruitment rate of southern fox squirrels was much lower than those of the eastern gray squirrel. Southern fox squirrel recruitment was lower in 2019 compared to those of 2016 and 2017. Southern fox squirrel recruitment was greater than recruitment estimates obtained for red squirrels at sites that consisted of both eastern gray squirrel and red squirrels. Eastern gray squirrels were present on MCDRPI, and my results suggest that recruitment rates of southern fox squirrels were less effected by the presence of eastern gray squirrels compared to red squirrel recruitment rates. It also suggests that recruitment rates of southern fox squirrels are low compared to the eastern gray squirrel, but greater than that of the red squirrel. Recruitment of translocated populations of Delmarva fox squirrels (*Sciurus niger cinereus*) in Maryland were measured using the number of lactating females captured through live-trapping at least five years post-translocation (Therres & Willey, 2002). On average 1 to 2 lactating females were captured at each site during the study. The number of individuals released at each site was between 5 to 42 individuals, with some sites requiring supplemental releases of individuals. The number of individuals translocated onto MCRDPI was similar to the recommended number of individuals for the translocation of Delmarva fox squirrels, and our population included a supplemental release 1 year after the initial release as well (Fish & Service, 1993). In our study, we observed two pregnant females. Our observations suggest that recruitment of our southern fox squirrel population was similar to those of the translocated populations of Delmarva fox squirrels.

Annual survival varied between 2016, 2017 and 2019. Southern fox squirrel survival was greatest in 2019 compared to 2017 and 2016, and was consistent with our expectations (i.e., survival would be highest in 2019 as an established population as opposed to 2016 and 2017 during translocation). The estimate for 2016 was similar to a successful translocation on Hall Island, SC (Dawson et al., 2009) and those of established populations on Spring Island, SC (Lee et al., 2008) and Fort Bragg, NC (Prince & DePerno, 2014). The estimate was 0.29 lower than the translocated population on St. Phillips, Island, SC (Dawson et al., 2009), and 0.27 lower than the established population on Ichauway, GA (Conner, 2001). The survival estimate for 2017 was similar to the translocated population on Hall Island, SC (Dawson et al., 2009). It was 0.26, 0.39, and 0.46 lower than those of established populations on Fort Bragg (Prince & DePerno, 2014), Spring Island (Lee et al., 2008), and Ichauway (Conner, 2001), respectively, as well as 0.48 lower than the translocated population on St. Phillips Island (Dawson et al., 2009). The estimate from 2019 was higher than those estimated from successful translocation and established populations (Figure 4). Survival differences between translocation years (i.e., 2016, 2017) versus

2019 when SFS were established could reflect differences in awareness of food sources and/or predator populations. Differences could also reflect the impact of Hurricane Matthew during fall 2016. The hurricane could have removed possible refuge sites and decreased food availability. We failed to detect differences between adult and juvenile survival, which contradicts previous literature suggesting low juvenile survival (Thompson, 1978). The candidate model with the stage of the individuals as a covariate was not supported; in fact, it was the least supported model among the candidate models.

The accuracy of the number of individuals entering the population appears to be high when compared with the known number of individuals translocated in 2016 and 2017. The estimated number of individuals in 2016 was between 26 to 34 individuals with the lower end of the range being the actual number of individuals that were translocated on to the MCRDPI, with possibility for recruitment within that year. In 2017, number of individuals that were translocated onto the MCRDPI falls in the range of the estimate with room for in-situ recruitment within the year.

Survival in 2016 was similar to other translocated populations, whereas the 2017 survival estimate was low in comparison. The survival rate in 2019, when the population had been established, was significantly higher than other established and translocated populations. Estimated juvenile recruitment rate of the MCRDPI population was low compared to those of the eastern gray squirrel but was greater than the red squirrel at sites where eastern gray squirrels were present. Our results indicated translocation as an efficient conservation tool for the long-term conservation of SFSs, as survival increased significantly after the two years post-translocation and recruitment of our fox squirrel population was similar to those of the Delmarva fox squirrel, for whom their successful delisting can be attributed to its many successfully translocated populations. Future studies examining the population dynamics of tree squirrels should consider estimating juvenile recruitment rates of the population, as it is an important component to assess a population trajectory. Further research is needed to understand the population dynamics of the SFS compared to other tree squirrel’s.

REFERENCES

Amspacher, K. M. (2018). *Southern fox squirrel (Sciurus niger niger) translocation, occupancy, and foraging behaviors.* (Master's thesis). Marshall University, (1180).

Arenz, C. L., & Leger, D. W. (1997). Artificial visual obstruction, antipredator vigilance, and predator detection in the thirteen-lined ground squirrel (Spermophilus tridecemlineatus). *Behaviour, 134*(13-14), 1101-1114.

Bendel, P. R., & Therres, G. D. (1994). Movements, site fidelity and survival of Delmarva fox squirrels following translocation. *American Midland Naturalist*, 227-233.

Benton, T. G., Plaistow, S. J., & Coulson, T. N. (2006). Complex population dynamics and complex causation: devils, details and demography. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1591), 1173-1181.

Bouskila, A. (1995). Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology*, *76*(1), 165-178.

Bowers, M., Jefferson, J., & Kuebler, M. (1993). Variation in giving-up densities of foraging chipmunks (Tamias striatus) and squirrels (Sciurus carolinensis). *Oikos*, 229-236.

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of computational and graphical statistics, 7*(4), 434-455.

Brown, B. W., & Batzli, G. O. (1984). Habitat selection by fox and gray squirrels: a multivariate analysis. *The Journal of Wildlife Management*, *48*(2), 616-621.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral ecology and sociobiology, 22*(1), 37-47.

Brown, J. S. (1992). *Patch use under predation risk: I. Models and predictions.* Paper presented at the Annales Zoologici Fennici.

Brown, J. S., & Alkon, P. U. (1990). Testing values of crested porcupine habitats by experimental food patches. *Oecologia, 83*(4), 512-518.

Brown, J. S., Arel, Y., Abramsky, Z., & Kotler, B. P. (1992). Patch use by gerbils (Gerbillus allenbyi) in sandy and rocky habitats. *Journal of mammalogy, 73*(4), 821-829.

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology letters, 7*(10), 999-1014.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of mammalogy, 80*, 385-399. doi:10.2307/1383287

Brown, J. S., Morgan, R. A., & Dow, B. D. (1992). *Patch use under predation risk: II. A test with fox squirrels, Sciurus niger.* Paper presented at the Annales Zoologici Fennici.

Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. *Model selection and multimodel inference, 2nd ed.* Springer, New York, 2.

Conner, L. M. (2001). Survival and cause-specific mortality of adult fox squirrels in southwestern Georgia. *The Journal of Wildlife Management,* 200-204.

Conner, L. M., Landers, J. L., Michener, W. K., Jones, J. W., Landers, J. L., & Michener, W. K. (1999). Fox Squirrel and Gray Squirrel Associations within Minimally Disturbed Longleaf Pine Forests. *Proc. Southeast. Assoc. of Fish and Wildl. Agencies, 53*, 364-374.

Cooch, E. (2008). Program MARK. “A gentle introduction.” *http://www.phidot. org/software/mark/docs/book/.*

Creel, S., Christianson, D., Liley, S., & Winnie, J. A. (2007). Predation risk affects reproductive physiology and demography of elk. *Science, 315*(5814), 960-960.

Dawson, J. R., Lee, J. C., Osborn, D. A., & Miller, K. V. (2009). Survival, Movements and Habitat Use of Translocated Southern Fox Squirrels. *The American midland naturalist, 162*, 335-345. doi:10.1674/0003-0031-162.2.335

Day, G. I., Schemnitz, S. D., & Taber, R. D. (1980). *Capturing and marking wild animals*. In *Wildlife Management Techniques Manual*. Bethesda, MD, U.S.A: The Wildlife Society.

Dudeck, B. P., Clinchy, M., Allen, M. C., & Zanette, L. Y. (2018). Fear affects parental care, which predicts juvenile survival and exacerbates the total cost of fear on demography. *Ecology, 99*, 127-135. doi:10.1002/ecy.2050

Edwards, J. W., Heckel, D. G., & Guynn, Jr., D. C. (1998). Niche overlap in sympatric populations of fox and gray squirrels. *The Journal of Wildlife Management*, 354-363.

Fish, U. S., & Service, W. (1993). Delmarva fox squirrel (Sciurus niger cinereus) recovery plan. 2nd revision. In: United States Fish and Wildlife Service Hadley, Massachusetts.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*(11), 1325-1330.

Frost, C. C. (1993). Four centuries of changing landscape patterns in the longleaf pine ecosystem. *Proceedings of the Tall Timbers Fire Ecology Conference*.

Goetz, S. M., Petersen, C. E., Rose, R. K., Kleopfer, J. D., & Savitzky, A. H. (2016). Diet and foraging behaviors of timber rattlesnakes, Crotalus horridus, in eastern Virginia. *Journal of Herpetology, 50*(4), 520-526.

Greene, D. U., & McCleery, R. A. (2017). Multi-scale responses of fox squirrels to land-use changes in Florida: Utilization mimics historic pine savannas. *Forest Ecology and Management, 391*, 42-51. doi:10.1016/j.foreco.2017.02.001

Griffith, B., Scott, J. M., Carpenter, J. W., & Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science, 245*(4917), 477-480.

Hughes, J. J., & Ward, D. (1993). Predation risk and distance to cover affect foraging behaviour in Namib Desert gerbils. *Animal behaviour*.

Jackson, J. A. (1971). The evolution, taxonomy, distribution, past populations and current status of the red-cockaded woodpecker. *Ecology and management of the redcockaded woodpecker. US Bureau of Sport Fishing and Wildlife and Tall Timbers Research Station, Tallahassee, FL*, 4-29.

James, F. C., & Shugart Jr, H. H. (1970). A quantitative method of habitat description. *Audubon Field Notes, 24*(6), 727-736.

Kellner, K. (2015). jagsUI: a wrapper around rjags to streamline JAGS analyses. *R package version, 1*(1).

Kéry, M., & Schaub, M. (2011). *Bayesian population analysis using WinBUGS: a hierarchical perspective*: Academic Press.

Koprowski, J. L. (2001). *North American Tree Squirrels*: Washington: Smithsonian Institution Press.

Kotler, B. P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology, 65*(3), 689-701.

Kotler, B. P., Brown, J. S., & Hasson, O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology, 72*(6), 2249-2260.

Kovacik, C. F., & Winberry, J. J. (2019). *South Carolina: a geography*: Routledge.

Laake, J. L. (2013). RMark: an R interface for analysis of capture-recapture data with MARK.

Landers, J. L., Van Lear, D. H., & Boyer, W. D. (1995). The longleaf pine forests of the southeast: requiem or renaissance? *Journal of Forestry, 93*, 38-44.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology, 79*, 1401-1409. doi:10.1139/z01-094

Lee, J. C. (1999). *Ecology of the southern fox squirrel on Spring Island, South Carolina.* University of Georgia.

Lee, J. C., Osborn, D. A., & Miller, K. V. (2008). Characteristics of a High Density Population of Southern Fox Squirrels. *The American midland naturalist, 159*, 385-393. doi:10.1674/0003-0031(2008)159[385:coahdp]2.0.co;2

Lima, S. L. (1992). Vigilance and foraging substrate: anti-predatory considerations in a non-standard environment. *Behavioral ecology and sociobiology, 30*(3-4), 283-289.

Lima, S. L. (1993). Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *The Wilson Bulletin*, 1-47.

Lima, S. L. (1998). Nonlethal Effects in the Ecology of Predator-Prey Interactions. *Bioscience, 48*, 25-34. doi:10.2307/1313225

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology, 68*, 619-640. doi:10.1139/z90-092

MacLeod, K. J., Krebs, C. J., Boonstra, R., & Sheriff, M. J. (2018). Fear and lethality in snowshoe hares: the deadly effects of non-consumptive predation risk. *Oikos, 127*, 375-380. doi:10.1111/oik.04890

McConnell, M. D., Monroe, A. P., Chandler, R., Palmer, W. E., Wellendorf, S. D., Burger, Jr., L. W., & Martin, J. A. (2018). Factors influencing Northern Bobwhite recruitment, with implications for population growth. *The Auk: Ornithological Advances, 135*(4), 1087-1099.

Meehan, K., & Jodice, P. G. (2010). Landscape Scale Correlates of Fox Squirrel Presence on Golf Courses in Coastal South Carolina. *Southeastern Naturalist, 9*(3), 573-586.

Moser, W. K., Jackson, S. M., Podrazsky, V., & Larsen, D. R. (2002). Examination of stand structure on quail plantations in the Red Hills region of Georgia and Florida managed by the Stoddard–Neel system: an example for forest managers. *Forestry, 75*(4), 443-449.

Newman, J. A., Recer, G. M., Zwicker, S. M., & Caraco, T. (1988). Effects of predation hazard on foraging “constraints”: patch-use strategies in grey squirrels. *Oikos*, 93-97.

Noss, R. F. (1989). Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal, 9*, 211-213.

Noss, R. F., Platt, W. J., Sorrie, B. A., Weakley, A. S., Means, D. B., Costanza, J., & Peet, R. K. (2015). How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions, 21*(2), 236-244.

Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., & Packer, C. (2017). A ‘dynamic’ landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology letters, 20,* 1364-1373. doi:10.1111/ele.12832

Peers, M. J., Majchrzak, Y. N., Neilson, E., Lamb, C. T., Hämäläinen, A., Haines, J. A., . . . Boonstra, R. (2018). Quantifying fear effects on prey demography in nature. *Ecology, 99*(8), 1716-1723.

Perkins, M. W., & Conner, L. M. (2004). Habitat Use of Fox Squirrels in Southwestern Georgia. *Journal of Wildlife Management, 68,* 509-513. doi:10.2193/0022-541x(2004)068[0509:huofsi]2.0.co;2

Peterson, R. (2017). Estimating normalization transformations with bestNormalize. *URL Httpsgithub CompetersonRbestNormalize*.

Peterson, R. A., & Cavanaugh, J. E. (2019). Ordered quantile normalization: a semiparametric transformation built for the cross-validation era. *Journal of Applied Statistics*, 1-16.

Plummer, M. (2015). JAGS Version 4.0. 0 user manual. *See https://sourceforgenet/projects/mcmc-jags/files/Manuals/4x*.

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: convergence diagnosis and output analysis for MCMC. *R news*, *6*(1), 7-11.

Potash, A. D., Conner, L. M., & McCleery, R. A. (2019). Vertical and horizontal vegetation cover synergistically shape prey behaviour. *Animal behaviour*, *152*, 39-44.

Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. *Ecology, 88*(11), 2744-2751.

Preston, C. R. (1990). Distribution of raptor foraging in relation to prey biomass and habitat structure. *The Condor, 92*(1), 107-112.

Prince, A., Chitwood, M. C., Lashley, M. A., DePerno, C. S., & Moorman, C. E. (2016). Resource selection by southeastern fox squirrels in a fire-maintained forest system. *Journal of mammalogy, 97*(2), 631-638.

Prince, A., & DePerno, C. S. (2014). Survival and Home-Range Size of Southeastern Fox Squirrels in North Carolina. *Southeastern Naturalist*, *13*, 456. doi:10.1656/058.013.0305

R Development Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological conservation, 102*(3), 227-234.

Rockwood, L. L. (2015). *Introduction to population ecology*: John Wiley & Sons.

Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*: Elsevier.

Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology, 88*(7), 1813-1823.

Sexton, O. J. (1990). Replacement of fox squirrels by gray squirrels in a suburban habitat. *American Midland Naturalist*, 198-205.

Sovie, A. R., Greene, D. U., & McCleery, R. A. (2020). Woody cover mediates fox and gray squirrel interactions. *Frontiers in Ecology and Evolution, 8,* 239.

Sperry, J. H., Peak, R. G., Cimprich, D. A., & Weatherhead, P. J. (2008). Snake activity affects seasonal variation in nest predation risk for birds. *Journal of Avian Biology, 39*(4), 379-383.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University.

Tappe, P. A., & Guynn, Jr., D. C. (1998). Southeastern fox squirrels: R-or K-selected? Implications for management. *Ecology and Evolutionary Biology of Tree Squirrels, MA Steele, JF Merritt and DA Zegers editors. Special Publication, 6,* 239-247.

Team, R. C. (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2012) ISBN 3-900051-07-0. *www.R-project. org*.

Therres, G. D., & Willey, Sr., G. W. (2002). *Reintroductions of the endangered Delmarva fox squirrel in Maryland.* Paper presented at the Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies.

Thierry, A., Beckerman, A. P., Warren, P. H., Williams, R. J., Cole, A. J., & Petchey, O. L. (2011). Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic and Applied Ecology, 12*(7), 562-570.

Thompson, D. C. (1978). Regulation of a northern grey squirrel (Sciurus carolinensis) population. *Ecology, 59*(4), 708-715.

Thorson, J. M., Morgan, R. A., Brown, J. S., & Norman, J. E. (1998). Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behavioral Ecology, 9,* 151-157. doi:10.1093/beheco/9.2.151

Tucker, Jr., J. W., Robinson, W. D., & Grand, J. B. (2004). Influence of fire on Bachman's Sparrow, an endemic North American songbird. *The Journal of Wildlife Management, 68*(4), 1114-1123.

U.S.D.A. (1980). *Soil Survey of Beaufort and Jasper Counties, South Carolina*. Soil Conservation Service. Washington D.C.

Van Der Merwe, M., Brown, J. S., & Jackson, W. M. (2005). The coexistence of fox (Sciurus niger) and gray (S. caroliniensis) squirrels in the Chicago metropolitan area. *Urban Ecosystems, 8*(3-4), 335.

Wall, W. A., Hoffmann, W. A., Wentworth, T. R., Gray, J. B., & Hohmann, M. G. (2012). Demographic effects of fire on two endemic plant species in the longleaf pine-wiregrass ecosystem. *Plant Ecology, 213*(7), 1093-1104.

Wauters, L. A., Lurz, P. W., & Gurnell, J. (2000). Interspecific effects of grey squirrels (Sciurus carolinensis) on the space use and population demography of red squirrels (Sciurus vulgaris) in conifer plantations. *Ecological Research, 15*(3), 271-284.

Weigl, P. D., Steele, M. A., Sherman, L. J., Ha, J. C., & Sharpe, T. L. (1989). The ecology of the fox squirrel (Sciurus niger) in North Carolina: implications for survival in the Southeast. *Bulletin-Tall Timbers Research Station, Tallahassee*.

White, G. C., & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird study, 46*(sup1), S120-S139.

Williams, C. K. (2013). Accounting for wildlife life-history strategies when modeling stochastic density-dependent populations: a review. *The Journal of Wildlife Management, 77*(1), 4-11.

Ydenberg, R. C., Brown, J. S., & Stephens, D. W. (2007). *Foraging: behavior and ecology*: University of Chicago Press.

Zanette, L. Y., White, A. F., Allen, M. C., & Clinchy, M. (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science, 334*(6061), 1398-1401.

APPENDIX A: IRB APPROVAL LETTER

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Office of Research Integrity

November 18, 2020

John Huang
3049 Sedgwick Ave
Bronx, NY 10468

Dear Mr. Huang:

This letter is in response to the submitted thesis abstract entitled *"Southern Fox Squirrel (Sciurus Niger Niger) Foraging Behavior and Population Dynamics."* 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 protocols #633 and #704. 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, ThLi, UiP
Director

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