ABSTRACT

PRINCE, ANNEMARIE. Habitat Selection, Survival, and Home Range Size of the Southeastern Fox Squirrel. (Under the direction of Christopher Moorman and Christopher DePerno.)

Fire-dependent longleaf pine forests of the southeastern United States are an important forest type for southeastern fox squirrels (*Sciurus niger niger*), a species of high conservation priority in the region. Prescribed fire is used as a land management tool to maintain the ecological integrity of southeastern longleaf pine forest systems. Historically, dormant-season prescribed burning was common, but in an effort to mimic natural fire regimes, resource managers have transitioned to more growing-season burns. Growing-season burns may reduce hardwood trees within longleaf pine forests and because a large percentage of the fox squirrel diet is hard mast, a reduction in hardwoods could reduce habitat quality for squirrels. To investigate relationships between growing-season prescribed fire and fox squirrel habitat selection we captured and radiocollared southeastern fox squirrels on Fort Bragg, North Carolina, USA. We used compositional analysis to assess fox squirrel home range selection and used resource utilization functions (RUFs) to investigate relationships between specific habitat covariates (i.e., trees/ha, distance to road, number of growing-season fires) and within home range habitat selection of fox squirrels. When selecting home ranges on Fort Bragg, fox squirrels selected southern yellow pine (i.e., primarily longleaf pine types) over other cover types. Within the home range, fox squirrels selected areas in close proximity to riparian zones.

Because most studies have focused on habitat use and not population demographics, we estimated survival rates using the Kaplan-Meier staggered entry design. Also, we calculated composite and seasonal 99% kernel density home range estimates for male and female fox squirrels. During our study, 22 radiocollared fox squirrels died; 8 were depredated, 2 were hunter harvested, and 12 died of unknown causes. Survival rates differed among the seasons when the sexes were combined (X^2 = 11.61, P = 0.03); survival was greatest in the winter and lowest in the fall. Male annual survival (0.35, 95% CI = 0.07 – 0.63) was lower than female annual survival (0.66, 95% CI = 0.41 – 0.91), but the statistical difference was weak (X^2 = 2.64, P = 0.10). Male home ranges were larger than female home ranges (F_1 = 14.257, P < 0.001), potentially exposing them to greater predation risk. High mortality of male fox squirrels may warrant reevaluation of harvest regulations for declining, hunted southeastern fox squirrel populations. In addition, large space requirements and concentrated use near riparian areas may be indicative of patchy forage availability on the landscape.

Habitat Selection, Survival, and Home Range Size of the Southeastern Fox Squirrel

by
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DEDICATION

To my mother, who encourages me to always see the beauty in everything wild.

BIOGRAPHY

Annemarie Prince was born and raised in Lake Wales, FL. She graduated with a Bachelor's degree in Wildlife Ecology from the University of Florida in 2004 and immediately started her career as a wildlife biologist. Annemarie has worked seasonal positions with the National Park Service and The Nature Conservancy, and has held permanent positions with the Florida Fish and Wildlife Conservation Commission and the Washington Department of Fish and Wildlife. After completing her Master's degree, Annemarie headed back west and is currently a biologist with the Washington Department of Fish and Wildlife.

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TABLE OF CONTENTS

LIST OF TABLES vi

LIST OF FIGURES vii

CHAPTER 1 Resource Selection By Southeastern Fox Squirrels In A Fire-Maintained Forest System 1

ABSTRACT 1

INTRODUCTION 3

STUDY AREA 5

METHODS 6
Animal Capture and Monitoring 6
Data Analysis 7

RESULTS 10

DISCUSSION 11

MANAGEMENT IMPLICATIONS 12

ACKNOWLEDGMENTS 13

LITERATURE CITED 14

CHAPTER 2 Survival and Home Range Size of Southeastern Fox Squirrels in North Carolina 25

ABSTRACT 25

INTRODUCTION 26

FIELD-SITE DESCRIPTION 27

METHODS 28
Animal Capture and Monitoring 28
Data Analysis 29

RESULTS 31

DISCUSSION 32

MANAGEMENT IMPLICATIONS 33

ACKNOWLEDGMENTS 34

LITERATURE CITED 35

LIST OF TABLES

CHAPTER 1

Table 1. Descriptions and proportion of study area in each of 7 cover types used in second-order southeastern fox squirrel resource selection analysis on Fort Bragg, North Carolina, USA, 2011-2012………………………………….. 22

Table 2. Matrix and cover type selection rankings of second-order southeastern fox squirrel resource selection on Fort Bragg, North Carolina, USA, 2011-2012……………………………………………………………………23

Table 3. Standardized RUF coefficients for 48 southeastern fox squirrels and the number of individual squirrels with significant positive (+) and negative (-) use (*P* < 0.05) associated with each habitat variable on Fort Bragg, North Carolina, USA, 2011-2012………………………………………………..24

CHAPTER 2

Table 1. Kaplan-Meier seasonal survival rates (Ŝ) and 95% confidence intervals for male, female, and combined sexes of radiocollared Southeastern Fox Squirrels on Fort Bragg, North Carolina, USA, 1 May 2011-2 June 2012…………....39

Table 2. Mean home range sizes (ha) and standard error (SE) by sex and season for radiocollared Southeastern Fox Squirrels on Fort Bragg, North Carolina, USA, 2011-2012………………………………………………………………...40

LIST OF FIGURES

CHAPTER 2

Figure 1. Southeastern Fox Squirrel harvest and Southeastern Fox Squirrel and Eastern Gray Squirrel hunting attempts on Fort Bragg, North Carolina, USA, 1982 – 2011... 41

CHAPTER 1

Resource Selection By Southeastern Fox Squirrels In A Fire-Maintained Forest System

ABSTRACT

Southeastern fox squirrels (*Sciurus niger niger*) are a longleaf pine (*Pinus palustris*) specialist, and fire is believed to be essential to the sustainability of fox squirrel populations in the southeastern United States. Historically, dormant-season prescribed burning was used to manage the longleaf pine ecosystem; however, to mimic natural fire regimes resource managers have transitioned to more growing-season burns. The transition to growing-season burning retains the open forest conditions selected by southeastern fox squirrels. However, growing-season burns may reduce hardwood trees, and because a large percentage of the fox squirrel diet is hard mast, a reduction in hardwoods could reduce habitat quality for fox squirrels. We used compositional analysis to assess home range selection by 48 radiocollared fox squirrels on Fort Bragg, North Carolina, USA. Additionally, we used resource utilization functions (RUF) to investigate the influence of growing-season fire and other habitat covariates on habitat selection within home ranges. When selecting a home range, fox squirrels selected southern yellow pine over other cover types on the study area. Proximity to riparian areas was the only significant predictor ($t = -2.18$, $d.f. = 47$, $P = 0.03$) of fox squirrel habitat use in the population level RUF and indicated fox squirrel use increased with decreasing distance to riparian areas. However, for individual squirrels, significance and direction of habitat relationships varied. In the Southeast, growing-season fire maintains the characteristic park-like condition of longleaf pine stands, a condition consistently selected by fox squirrels. In upland pine stands where prescribed burning is common, riparian areas can shelter hardwoods from fire and provide seasonally important food resources for fox squirrels.

KEY WORDS: Fort Bragg, compositional analysis, habitat use, longleaf pine, North Carolina, prescribed fire, radio telemetry, *Sciurus niger*, utilization distribution.

INTRODUCTION

Fire-dependent longleaf pine (*Pinus palustris*) forests of the southeastern United States are important for southeastern fox squirrels (*Sciurus niger niger*; hereafter fox squirrel), a species of high conservation priority in the region (Weigl et al. 1989, Perkins et al. 2008). Declines in fox squirrel populations have coincided with the degradation and loss of mature longleaf pine forests, which now occupy less than 3% of the original extent (Weigl et al. 1989, Kantola and Humphrey 1990, Loeb and Moncrief 1993, Landers et al. 1995, Perkins and Conner 2004). The drastic reduction of longleaf pine forests is credited to widespread timber harvest occuring at the turn of the 20th century, rapid urbanization of the eastern US, conversion to slash (*Pinus elliottii*) or loblolly (*Pinus taeda*) pine plantations, and fire suppression (Frost 1993, Landers et al. 1995, Outcalt and Sheffield 1996).

The longleaf pine forest is characterized by widely spaced longleaf pine trees, scattered hardwood patches, and diverse understory vegetation (Frost 2006). Large, mature pine and hardwood trees provide important seasonal food resources for fox squirrels (Moore 1957, Ha 1983, Kantola 1986, Weigl et al 1989). Additionally, large hardwood trees serve as refugia and nesting sites and provide cavities for rearing young (Moore 1957, Weigl et al 1989, Kantola 1992, Conner and Godbois 1993). However, compared to longleaf pine, hardwood species are less tolerant of fire. Therefore, the extent of hardwoods is limited by frequent fires, and hardwoods often naturally occur on fire-maintained properties only as individual canopy trees or in small isolated patches within the pine matrix (Greenberg and Simons 1999).

In much of the Southeast, the focus of contemporary restoration and management of longleaf pine forests is reduction of hardwood species that have invaded pine uplands as a result of fire suppression (Provencher et al. 2001, Kush et al. 2004, Varner at al. 2005). In many cases, land managers use machinery, herbicides, and growing-season fire to achieve and maintain hardwood-free upland pine forests (Boyer 1990, Means 1996, Provencher et al. 2001, Varner et al. 2005). However, a pure pine forest may not be representative of pre-settlement conditions, where 33% of longleaf pine stands were actually mixed pine-hardwood stands (Frost 1993). Historically, variation in fire regime and intensity allowed large canopy hardwood trees and isolated patches of smaller hardwood trees to persist at 10–60 trees per hectare within pine-hardwood forests (Moore 1957, Frost 1993, Rebertus et al. 1993, Greenberg and Simons 1999).

Though resource managers currently use dormant-season and growing-season prescribed fire to restore and maintain longleaf pine forests, some prescribed fire programs within the Southeast are beginning to emphasize the timing of natural fires (i.e., lighting ignited) and are shifting to the use of more growing-season prescribed fire (Cantrell et al. 1995, Fill et al. 2012). Frequent, growing-season prescribed fires maintain the open forest conditions required by fox squirrels, but these burns can reduce the prevalence of mature hardwoods within longleaf pine forests (Robbins and Myers 1992). Because fox squirrels rely heavily on acorns and other hard mast for a large percentage of their diet, the negative effects of fire on oaks (*Quercus* spp.) and the subsequent decreased availability of hard mast could be limiting fox squirrel populations (Baumgartner 1940, Allen 1943, Weigl et al. 1989, Kantola and Humphrey 1990, Greenberg and Simons 1999). Conversely, in the absence of frequent fires, longleaf pine communities shift from open canopy forests to closed canopy systems dominated by shade-tolerant and fire-sensitive plant species (Heyward 1939, Garren 1943, Nowacki and Abrams 2008), a condition more suitable for the eastern gray squirrel (*Sciurus carolinensis*) (Edwards et al. 1998, Whitaker and Hamilton 1998).

Currently, there is limited information on the impacts of prescribed burning on fox squirrels. Although prescribed burning commonly is recommended for managing fox squirrel habitat, these recommendations often do not specify a season or frequency of how prescribed burns should be applied (Weigl et al. 1989, Conner et al. 1999, Conner and Godbois 2003, Perkins and Conner 2004). Our objective was to evaluate the influence of frequent growing-season prescribed burns on fox squirrel habitat selection at 2 levels: home-range selection (second-order selection) and within home-range selection (third-order selection, Johnson 1980).

STUDY AREA

Fort Bragg Military Installation is a 64,280-ha active army base in the Sandhills physiographic region of North Carolina, United States. Dominated by an overstory of longleaf pine and an understory of wiregrass (*Aristida stricta*), Fort Bragg and other adjacent areas formed the largest contiguous tract of longleaf pine-wiregrass ecosystem remaining in North Carolina (Sorrie et al. 2006). Large hardwood trees, including turkey oak (*Q. laevis*), sand post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), southern red oak (*Q.*

falcata), and hickory (*Carya* spp.), were scattered across the base and were present in small patches in the uplands, along riparian areas, and bordering parachute drop zones. Fort Bragg's land managers heavily used prescribed fire to maintain an open forest midstory for the federally endangered red-cockaded woodpecker (*Picoides borealis*). Beginning in 1989, prescribed fires were conducted primarily in the growing-season (April – June) every three years to prevent hardwood encroachment in the uplands; however, dormant season burns were conducted yearly on the parachute drop zones and throughout the base on forest acreage not burned due to weather or lack of personnel the previous year (Jeff Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.). Hunters on Fort Bragg were allowed to harvest 1 fox squirrel per day with a season limit of 10 from October – December. According to Fort Bragg harvest records, squirrel hunter effort decreased on Fort Bragg since 1982, but fox squirrel harvest remained relatively constant with an increasing trend since 2008; on average, 78 fox squirrels were harvested on Fort Bragg from 2001 – 2011 (Jeff Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.).

METHODS

Animal Capture and Monitoring

We trapped fox squirrels using wooden box traps (Baumgartner 1940) and wire-cage traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) baited with dried whole kernel corn. Trap locations were chosen based on capture success of traps placed randomly by Scott (2011). Once captured, we transferred fox squirrels into a modified capture cone (Koprowski 2002). We weighed, sexed, aged (juvenile or adult, Weigl et al. 1989), assessed for reproductive condition, and individually ear-tagged (Monel 1005-1/1005-3, National Band and Tag Company, Newport, Kentucky, USA) all captured fox squirrels. We radiocollared adult fox squirrels weighing >750 g (collar weight 19 g, ≤3% body weight; Model SI-2C, Holohil Sys. Ltd., Ontario, Canada) and released them at the capture location. We had 33 radiocollars available for deployment, and we trapped periodically from February 2011 – May 2012 to maintain 33 radiocollared fox squirrels throughout the study. All capture and processing methods met the specifications set forth by the Institutional Animal Care and Use Committee at North Carolina State University (IUCUC # 10-153-O) and followed guidelines of the American Society of Mammalogists (Gannon and Sikes 2007).

We located radiocollared fox squirrels once per day and at least 3 times per week using the homing technique at random times between 0.5 hours after sunrise and 0.5 hours before sunset (White and Garrott 1990). We continually monitored radiocollared fox squirrels until death, radio failure, or they became inaccessible to tracking (i.e., moved into artillery impact area). We recorded all fox squirrel locations using a handheld global positioning system (Rino120, Garmin International, Inc., Olathe, Kansas, USA).

Data Analysis

We assessed second-order habitat selection (Johnson 1980) using compositional analysis (Aebischer et al. 1993) as modified by Millspaugh et al. (2006); we compared cover types available within the study area to a utilization distribution (UD)-weighted estimate of habitat use within the home range. We included fox squirrels with ≥30 locations for our study period

(March 2011 – June 2012) in the analysis. Individual animals were treated as the sampling unit and all cover types were considered simultaneously. Cover type data was from the North Carolina Corporate Geographic Database (Earth Satellite Corporation 1997). We used 7 cover types based on dominant vegetation: southern yellow pine (i.e., primarily longleaf pine), bottomland hardwood forest, managed herbaceous cover, mixed hardwood/conifers, mixed shrubland, mixed upland hardwoods, and upland herbaceous (Table 1). We estimated fixed kernel density home ranges using Geospatial Modeling Environment (GME, Version 0.7.1.0, Hawthorne L. Beyer 2009 – 2012)) and output UD grids with a 10-m X 10-m cell size. We used the bivariate plug-in option within GME to estimate the bandwidth for each squirrel's kernel density estimate (Wand and Jones 1995, Gitzen et al. 2006). We assigned use values based on the 95% UD, where the proportion of UD volume in each cover type represented an individual's habitat use within the home range (Millspaugh et al. 2006). The null hypothesis of no selection was tested using multivariate analysis of variance (Wilks' lambda). Rejection of the null hypothesis led to a series of paired *t*-tests that ranked cover types from most to least selected (Aebischer et al. 1993). We used the adehabitatHS package within program R to implement compositional analysis and to rank cover types within the study area (Calenge 2006, R Core Team 2012).

We evaluated habitat selection within each fox squirrel's home range (third-order selection, Johnson 1980) using the resource utilization function (RUF) approach (Marzluff et al. 2004). We related UDs to habitat covariates believed to influence fox squirrel habitat selection using multiple regression adjusted for spatial autocorrelation (Marzluff et al. 2004). Habitat covariates included number of large hardwood (≥26 cm dbh) trees per hectare, number of large pine (≥37 cm dbh) trees per hectare, number of growing-season burns in the previous 20 years, distance to nearest riparian area (m), and distance to nearest road (m). Roads included paved surfaces, unpaved surfaces, and firebreaks, and riparian areas were defined by the presence of permanent wetland vegetation (Fort Bragg GIS Database). We included fox squirrels with ≥30 locations for our study period (March 2011 – June 2012) in the RUF analysis. Using the isopleth command in GME, we converted each UD to 99% volume contour polygons, where contours represented 1 – 99 percentiles of use probabilities. We overlaid 30-m X 30-m sampling grids centered on the habitat raster layers on each percent volume polygon within ArcGIS10 (Environmental Systems Research Institute, Redlands, California, USA). We used the sample tool within ArcGIS10 to extract relative use values and covariates associated with each point in the sampling grid. From Fort Bragg personnel, we acquired GIS layers that contained all habitat covariates used in the analyses.

For RUF analysis, we used the ruf package within program R (Handcock 2012, R Core Team 2012). We used each squirrel's bandwidth estimate from the bivariate plug-in as the starting point for estimating the range of spatial dependence, and used 1.5 for the smoothing estimate within the ruf.fit function. We evaluated the need for transformations by examining the residual plots from univariate RUFs for five randomly selected squirrels. We log transformed the response variable for all squirrels which normalized the response variable and residuals from the univariate RUFs.

We used all covariates to create RUFs for each squirrel and averaged the standardized coefficients to create a population level RUF. We used the relative use value as the dependent variable and the habitat covariates as the independent values in the multiple regression analysis. The magnitude and sign of the standardized coefficients indicated the importance of resources and the direction of use, respectively.

RESULTS

From January 2011 – May 2012, we captured 76 (28 F, 47 M, 1 Unk) fox squirrels on Fort Bragg and equipped 52 (20 F, 31 M, 1 Unk) with radiocollars. Forty-eight fox squirrels (22 F, 25 M, 1 Unk) had sufficient relocations to include in the selection analysis. For fox squirrels included in the analysis, the number of relocations ranged from 30 to 208 and tracking times varied from 54 days to 452 days.

Fox squirrels used cover types on Fort Bragg in a nonrandom manner (Λ = 0.02, *d.f.* = 2, *P* = 0.001). The following order of selection was detected: southern yellow pine > mixed hardwood/conifer > bottomland hardwood > upland herbaceous > mixed shrubland > mixed hardwood > managed herbaceous (Table 2). However, the differences between mixed hardwood/conifer and bottomland hardwood, and upland herbaceous, mixed shrubland, mixed hardwood and managed herbaceous were not significant at α = 0.05.

Distance to riparian area was the only predictor (t = -2.18, *d.f.* = 47, *P* = 0.03) of fox squirrel habitat use in the population level RUF; use increased with decreasing distance to a riparian area (Table 3). Predictor variables were not consistently correlated with use among individual squirrels, and predictor variables varied in degree of importance among squirrels (Table 3).

DISCUSSION

On Fort Bragg, fox squirrels selected upland longleaf pine, a vegetation community that dominated the fire-maintained systems in which fox squirrels evolved (Weigl et al. 1989, Perkins and Conner 2004, Perkins et al. 2008). The fox squirrel's large body size is thought to be an adaptation for living in fire-maintained pine forests, affording them increased mobility, access to widely spaced food resources, and the ability to manipulate large longleaf pine cones (Steele 1988, Steele and Weigl 1993, Weigl et al. 1989). During summer months, fox squirrels feed heavily on the seeds within longleaf pine cones, commonly consuming between 20-30 cones per day (Steele 1988, Steele and Weigl 1993, Weigl et al. 1989,).

However, fox squirrels consistently selected areas with a hardwood component, likely because of the food and cover resources provided. Within longleaf pine stands, fox squirrels concentrated use near riparian areas, which likely supported less fire-intolerant hardwood species that produce seasonally important food resources (Hoctor et al. 2006). Perkins et al. (2008) suggested optimal fox squirrel habitat contained 88.2% mature pine cover and 11.8% hardwood cover and acknowledged the upland hardwood component could be lower if pine stands were adjacent to streams where hardwoods were more prevalent. Also, hardwood stands provide important refuge sites and nesting sites for fox squirrels, and of our radiocollared squirrel nest locations, 42% were in hardwood species (A. Prince, unpublished data).

Because hardwoods provide important food and cover resources, frequent fires that limit the abundance and distribution of hardwoods could be affecting fox squirrel survival and/or reproductive success (Conner and Godbois 1993, Weigl et al. 1989). Nesting sites can include natural cavities and leaf nests, and are critical to squirrels for a variety of reasons, including protection against predators and shelter from poor weather conditions (Moore 1957, Baumgartner 1939, Nixon et al. 1984). In North Carolina, squirrels used artificial cavities (nest boxes) more often in rainy or cold weather and during periods of low food supply (Weigl 1989). Weigl et al. (1989) suggested that a lack of cavities for rearing young in upland areas was limiting fox squirrel populations in North Carolina. Evaluating the impacts of frequent growing-season prescribed fire on fox squirrel reproductive success could help assess whether relegation of hardwood stems to riparian areas provides the essential resources (i.e., food and cover) necessary for sustaining fox squirrel populations.

MANAGEMENT IMPLICATIONS

Frequent fires applied to upland pine stands on Fort Bragg likely benefited fox squirrels by preventing the succession of open pine dominated uplands to high-density hardwood stands favored by gray squirrels. However, maintaining some (historically 10-60 per ha) mature hardwood trees that are accessible to fox squirrels is critical. When developing a fire program, resource managers should strive to leave burns patchy allowing for the regeneration and maturation of hardwoods. A frequent growing-season fire regime that suppresses hardwoods within upland pine stands should be balanced with low intensity fires in riparian areas that shelter fire-intolerant hardwood species. If riparian areas with canopy level hardwoods are not widely distributed across a site, managers should leave mature hardwoods scattered throughout upland pine stands.

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Table 1. Descriptions and proportion of study area in each of 7 cover types used in second-order southeastern fox squirrel resource selection analysis on Fort Bragg, North Carolina, USA, 2011- 2012 (Earth Satellite Corporation 1997).

Cover type	Description	% of study area
Bottomland Hardwoods	Lowland areas with deciduous dominant woody vegetation ≥ 3 m in height and crown density ≥ 25%.	9%
Managed Herbaceous Cover	Actively managed areas of herbaceous cover, including drop zones and artillery firing points.	2%
Mixed Hardwoods/ Conifers	Areas with ≥ 25% intermixture of deciduous and evergreen species. Hardwoods constitute a plurality of stocking, but pines account for 25 to 50% of the stocking.	4%
Mixed Shrubland	Areas with vegetation (evergreen and/or deciduous) dominated by shrubs and/or woody plants < 3 m in height.	4%
Mixed Hardwoods	Upland areas with deciduous dominant woody vegetation > 3 m in height and crown density ≥ 25%.	2%
Southern Yellow Pine	Forested areas with 75% pine, including longleaf pine, loblolly-slash pine, and/or pond pine.	73%
Upland Herbaceous	Unmanaged upland areas covered by herbaceous vegetation.	5%

Table 2. Matrix and cover type selection rankings of second-order southeastern fox squirrel resource selection on Fort Bragg, North Carolina, USA, 2011-2012. The sign of the *t*-statistic is indicated with + or – signs; +++ and --- represent significant deviation from zero.

	Cover type							
Cover type	**Bottomland Hardwood**	**Managed Herbaceous**	**Mixed Hardwood/ Conifer**	**Mixed Shrubland**	**Mixed Hardwood**	**Southern Yellow Pine**	**Upland Herbaceous**	**Rank**
Bottomland Hardwood	•	+++	-	+++	+++	---	+++	3
Managed Herbaceous	---	•	---	+	+++	---	-	7
Mixed Hardwood/ Conifer	+	+++	•	+++	+++	---	+++	2
Mixed Shrubland	---	-	---	•	+	---	-	5
Mixed Hardwood	---	---	---	-	•	---	---	6
Southern Yellow Pine	+++	+++	+++	+++	+++	•	+++	1
Upland Herbaceous	---	+	---	+	+++	---	•	4

Table 3. Standardized RUF coefficients for 48 southeastern fox squirrels and the number of individual squirrels with significant positive (+) and negative (-) use (*P* < 0.05) associated with each habitat variable on Fort Bragg, North Carolina, USA, 2011 – 2012.

				Number of individuals	
Variable	Standardized $\bar{\beta}$	95% CI	$P\ (\bar{\beta} = 0)$	+	-
Growing-season fires[a]	-0.010	-0.028, 0.008	0.277	3	4
Large hardwood trees/ha	0.003	-0.025, 0.030	0.860	2	0
Large pine trees/ha	0.011	-0.014, 0.035	0.415	3	2
Distance to road (m)	0.032	-0.009, 0.073	0.135	9	6
Distance to riparian area (m)	-0.057	-0.108, -0.006	0.035	4	13

[a] Number of fires in the last 20 years

CHAPTER 2

Survival and Home Range Size of Southeastern Fox Squirrels in North Carolina

ABSTRACT

Studies of *Sciurus niger* (Fox Squirrels) in the Southeast have focused on habitat relationships with limited emphasis on other life-history characteristics. We estimated survival rates for 51 radiocollared Southeastern Fox Squirrels (*S. n. niger*; hereafter Fox Squirrels) on Fort Bragg, North Carolina, USA from March 2011 – June 2012 using the Kaplan-Meier staggered entry design. Also, we calculated composite and seasonal 99% kernel density home range estimates for male and female Fox Squirrels. During our study, 22 radiocollared Fox Squirrels died; 8 were depredated, 2 were hunter harvested, and 12 died of unknown causes. Survival rates differed among the seasons when the sexes were combined ($X^2 = 11.61$, $P = 0.03$); survival was greatest in the winter and lowest in the fall. Male annual survival (0.35, 95% CI = 0.07 – 0.63) was lower than female annual survival (0.66, 95% CI = 0.41 – 0.91), but the statistical difference was weak ($X^2 = 2.64$, $P = 0.10$). Male home ranges were larger than female home ranges ($F_1 = 14.257$, $P < 0.001$), potentially exposing them to greater predation risk. High mortality of male Fox Squirrels may warrant reevaluation of harvest regulations for declining, hunted Fox Squirrel populations. Additionally, large space requirements may be indicative of low forage availability on the landscape, thus requiring land managers to adjust management actions to improve habitat conditions for Fox Squirrels.

INTRODUCTION

In the Southeast, most studies of *Sciurus niger* Linnaeus (Fox Squirrel) have focused on habitat relationships, and few have focused on demographic processes, including survival (Conner 2001, Lee et al. 2008, McCleery et al. 2008, Weigl et al. 1989). Yet, survival estimates are critical for setting appropriate hunting seasons and harvest limits where Fox Squirrels are hunted (Bailey 1984, Dasmann 1981).

In some southeastern states, Fox Squirrel and *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel) harvest regulations and bag limits are combined to form a general squirrel season (Loeb and Moncreif 1993, Tappe and Guynn 1998). Recently, researchers have questioned managing these species together because Fox and Gray Squirrels have different survival strategies (Conner 2001, Edwards et al. 2003, Lee et al. 2008, Tappe and Guynn 1998). In the Southeast, Fox Squirrels tend to be long-lived, have smaller and fewer litters, and exhibit high adult survival. Therefore, Tappe and Guynn (1998), and others (see Conner 2001, Lee et al. 2008), suggested Fox Squirrels are closer to a K-selected species (Pianka 1970) than Eastern Gray Squirrels and should be managed separately with respect to hunting seasons and harvest regulations.

Although mid-western Fox Squirrels have been more thoroughly studied, extrapolation of survival rates from these studies is not appropriate because of ecological differences between regional populations (e.g., diet, home range size, morphology, habitat use) (Conner 2001, Edwards et al. 1989, Nixon et al. 1968, Weigl et al. 1989). Therefore, we estimated survival rates for a population of Southeastern Fox Squirrels (*S.n. niger*; hereafter Fox Squirrels). Also, we estimated the seasonal and composite home range size of male and female Fox Squirrels to determine if home range size contributed to differences in survival rates between the sexes.

FIELD-SITE DESCRIPTION

We conducted the study on Fort Bragg Military Installation, a 64,280-ha active army base in the Sandhills physiographic region of North Carolina, United States. Dominated by an overstory of *Pinus palustris* Mill. (Longleaf Pine) and an understory of *Aristida stricta* Michx. (Wiregrass), Fort Bragg and adjacent areas make up the largest contiguous tract of Longleaf Pine-Wiregrass ecosystem remaining in North Carolina (Sorrie et al. 2006). Large hardwood trees, including *Quercus laevis* Walter (Turkey Oak), *Q. stellata* Ashe (Sand Post Oak), *Q. marilandica* Münchh. (Blackjack Oak), *Q. falcata* Michx. (Southern Red Oak), and *Carya* spp. (Lam. ex Poir.) Nutt. (Hickories), were scattered across the base and located in small patches in the uplands, along drainages, and bordering the military drop zones. Fort Bragg relied heavily on the use of prescribed fire to maintain an open midstory for the federally endangered *Picoides borealis* Vieillot (Red-cockaded Woodpecker). Beginning in the late 1980's, prescribed fires were conducted primarily in the growing-season (April – June) every 3 years to prevent hardwood encroachment in the uplands; however, dormant season burns were conducted yearly on the parachute drop zones and throughout the base on forest acreage not burned due to weather or lack of personnel the previous year (Jeff Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.). On Fort Bragg, hunters were allowed to harvest 1 Fox Squirrel per day with a season limit of 10 from October – December. The Eastern Gray Squirrel hunting season extended from October – February and had a daily limit of 8 with no season limit. Hunting Eastern Gray Squirrels and Fox Squirrels with dogs was permitted on Fort Bragg. Since 1982, squirrel hunter effort has declined on Fort Bragg and Fox Squirrel harvest has been variable (Jeff Jones, Fort Bragg Wildlife Branch, Fort Bragg, NC, pers. comm.; Fig. 1).

METHODS

Animal Capture and Monitoring

We trapped Fox Squirrels using wooden box traps (Baumgartner 1940) and wire-cage traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) baited with dried whole kernel corn. After capture, Fox Squirrels were transferred into a modified capture cone (Koprowski 2002) and weighed, sexed, aged (juvenile or adult; Weigl et al. 1989), assessed for reproductive condition, and individually ear-tagged (Monel 1005-1/1005-3, National Band and Tag Company, Newport, Kentucky, USA). We radiocollared adult Fox Squirrels weighing ≥750 g (collar weight 19 g, <3% body weight; Model SI-2C, Holohil Sys. Ltd., Ontario, Canada) and released them at the capture location. During the study, we had 33 radiocollars available for deployment, and we trapped periodically from February 2011 – May 2012 to maintain 33 radiocollared Fox Squirrels throughout the study. All capture and processing methods met the specifications set forth by the Institutional Animal Care and Use

Committee at North Carolina State University (IUCUC # 10-153-O) and followed guidelines of the American Society of Mammalogists (Gannon and Sikes 2007).

We located radiocollared Fox Squirrels once per day and ≥3 times per week using the homing technique (White and Garrott 1990) at random times between 0.5 hours after sunrise and 0.5 hours before sunset from February 2011 – June 2012. We continually monitored radiocollared Fox Squirrels until death, radio failure, or they became inaccessible to tracking (i.e., moved into artillery impact area).

We confirmed mortalities by the presence of Fox Squirrel remains near the radiocollar or when there was blood and/or bite marks on the radiocollar. We determined cause of death by examining squirrel remains and swabbing the radiocollar for potential predator DNA. We obtained DNA swabs by vigorously rubbing a double-sided Q-tip on the radiotransmitter and the collar casing. We individually labeled the swabs, placed them in envelopes, and sent them to Wildlife Genetics International (Nelson, Canada) for genetic analysis. The species identification test was a sequence-style analysis of the 16S rRNA mitochondrial gene (Johnson and O'Brien 1997). Using evidence from the field and from the laboratory DNA results, we categorized mortalities as predation (mammalian carnivores and raptors), hunting, and unknown.

Data Analysis

We excluded radiocollared Fox Squirrels that died within 7 days of capture to avoid using capture related mortalities in our analysis (Conner 2001). Also, we censored Fox Squirrels when the radiocollar stopped transmitting, an individual moved into the artillery impact area (inaccessible to tracking), or when we found the collar with no clear sign of mortality.

We calculated annual and seasonal survival rates using the staggered entry modification (Pollock et al. 1989) of the Kaplan-Meier product limit survival estimator (Kaplan and Meier 1958). We estimated annual survival using 52 weeks of data collection. We defined seasons based on plant phenology and according to Weigl et al. (1989) (winter: 16 January to 15 March, spring: 16 March to 1 June, summer: 2 June to 30 September, and fall: 1 October to 15 January). We used a chi-square test within Program CONTRAST to compare seasonal survival rates for males, females, and the sexes combined, and annual survival rates between males and females (Sauer and Hines 1989); alpha was set at 0.05.

We calculated seasonal home ranges for Fox Squirrels using the same seasons defined above, and calculated composite home ranges for Fox Squirrels with ≥30 locations during the study period. We imported coordinates of squirrel locations into a geographic information system (ArcView10, Environmental Systems Research Institute, Redlands, CA) and calculated 99% kernel density home ranges using the kde function (bandwidth = PLUGIN, cell size = 30) within the Geospatial Modeling Environment (Version 0.7.1.0, Hawthorne L. Beyer 2009 – 2012). We used 2-way analysis of variance (ANOVA) and Tukey's HSD post hoc comparison tests to compare home ranges sizes between the sexes and among the seasons.

RESULTS

We radiomarked 52 Fox Squirrels (27M, 24F, 1Unk). The mean body weight at capture was 922 ± 22 g for males and 963 ± 24 g for females. One male Fox Squirrel was removed from the survival analysis because it died within 7 days of capture. We detected 22 mortalities (15M, 7F); 2 squirrels were harvested by hunters and 8 were killed by predators. Of the 8 predator mortalities, *Lynx rufus* Schreber (Bobcat) and *Urocyon cinereoargenteus* Schreber (Gray Fox) DNA were extracted from 1 collar each, we suspected a *Buteo jamaicensis* Gmelin (Red-tailed Hawk) killed 1 squirrel, and the remaining 4 deaths were not attributable to a specific predator. Twelve squirrels lacked sufficient remains to determine cause of death and were classified as unknown. However, because of the presence of the tail and fur at the recovered collar location, we suspect predation in 6 of the 12 deaths classified as unknown. Predation was the leading cause of death for male and female Fox Squirrels on Fort Bragg.

Survival rates differed among the seasons when the sexes were combined (X^2 = 11.61, P = 0.03); survival was greatest in the winter and lowest in the fall (Table 1). Male annual survival was lower than female annual survival, but the statistical difference was weak (X^2 = 2.64, P = 0.10).

Composite home ranges were calculated for 47 (25 M, 22 F) Fox Squirrels. Male composite home ranges (81.26 ± 14.12 ha [range 6.85 – 312.67 ha]) were larger (F_1 = 14.257, P < 0.001) than females (19.83 ± 3.01 ha [range 5.40 – 72.07 ha]) (Table 2). We observed an effect of season on home range size (F_3 = 5.78, P < 0.01), and spring home ranges were larger than in winter.

DISCUSSION

Our estimate of male annual survival was low compared to other studies in the Southeast and may be explained by the large home ranges of male Fox Squirrels on Fort Bragg and the resulting increase in predation risk. The Kaplan-Meier estimate of male annual survival on Fort Bragg was 0.35 (95% CI = 0.07 – 0.63) compared with 0.73 (95% CI = 0.59 – 0.87) and 0.62 (95% CI = 0.46 – 0.78) calculated for Fox Squirrel populations in Georgia (Conner 2001) and South Carolina (Lee et al. 2008), respectively. Discrepancies in predation rates among studies of Fox Squirrel survival could be due in part to differing forest structure on study sites or to varying predator densities across the Southeast. Weigl et al. (1989) suggested that Fox Squirrel predation would only reach appreciable levels when Fox Squirrel habitat was in close proximity to large closed-canopy hardwood stands that support high populations of alternate prey, like Eastern Gray Squirrels. Because Fox Squirrels on Fort Bragg selected areas in close proximity to drainages with high hardwood densities, Weigl's hypothesis could explain our relatively high predation rates and low male survival (Prince 2013). Regardless of the mechanism, low male survival estimates on Fort Bragg suggest the need for close monitoring of the potential additive effects of hunter harvest in the future.

Seasonal changes in activity level and home range size likely caused the variation in seasonal survival estimates for Fox Squirrels on Fort Bragg. In North Carolina, the spring and fall are typically seasons of plentiful food, and corresponding increases in foraging and caching behavior could make males and females more susceptible to predation (Edwards et al. 2003, Weigl et al. 1989). During our study, the majority of the Fox Squirrel mortalities occurred in the fall, but home range sizes for males and females were greatest in the spring. Perhaps squirrels are more active during the fall, but their movements are more localized as they forage in areas with a greater hardwood (and acorn) component. In contrast, survival rates were greatest in the winter and may correlate with reduced activity during this time period; decreased activity similarly was observed for Eastern Gray Squirrels in Maryland (Thompson 1977).

In all studies of Fox Squirrel space use in the Southeast, males consistently had larger home ranges; however, techniques used to determine home range size have varied (Edwards 1986, Powers 1993, Weigl et al. 1989, Wooding 1997). For example, previous studies in the Southeast used the minimum convex polygon method for determining home range sizes and report estimates of the mean size ranging from 79.5 ha for male Fox Squirrels in Florida (Wooding 1997) to 11.6 ha for females in Alabama (Powers 1993). Home range estimates derived from kernel density estimators are considered more robust than minimum convex polygon methods and our comparatively large estimates may more accurately represent the true space requirements of Fox Squirrels.

MANAGEMENT IMPLICATIONS

For declining or isolated, hunted Fox Squirrel populations, a high mortality rate for male Fox Squirrels may warrant reevaluation of harvest regulations. Additionally, if large space requirements of Fox Squirrels are indicative of low forage availability on the landscape, land managers may need to adjust management actions to improve habitat conditions for Fox Squirrels.

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Table 1. Kaplan-Meier seasonal survival rates (Ŝ) and 95% confidence intervals for male, female, and combined sexes of radiocollared Southeastern Fox Squirrels on Fort Bragg, North Carolina, USA, 1 May 2011 – 2 June 2012.

Time Period[a]	**Males**			**Females**			**Combined**		
	Ŝ	**95% CI**		**Ŝ**	**95% CI**		**Ŝ**	**95% CI**	
		lower	**upper**		**lower**	**upper**		**lower**	**upper**
Spring ‘11	0.87	0.71	1.03	0.93	0.81	1.06	0.88	0.77	0.88
Summer ‘11	0.87	0.71	1.02	0.82	0.64	1.01	0.85	0.72	0.85
Fall ‘11	0.66	0.45	0.87	0.80	0.61	0.99	0.72	0.57	0.72
Winter ‘11	0.94	0.82	1.06	1.00	1.00	1.00	0.97	0.90	0.97
Spring ‘12	0.65	0.27	1.02	1.00	1.00	1.00	0.84	0.66	0.84
Annual[b]	0.35	0.07	0.63	0.66	0.41	0.91	0.49	0.30	0.68

[a] spring: 16 March to 1 June, summer: 2 June to 30 September, fall: 1 October to 15 January, winter: 16 January to 15 March

[b] 2 June 2011 – 2 June 2012

Table 2. Mean home range sizes (ha) and standard error (SE) by sex and season for radiocollared Southeastern Fox Squirrels on Fort Bragg, North Carolina, USA, 2011 – 2012.

Season[a]	**Males**			**Females**			**Combined**		
	N	**Home Range**	**SE**	**N**	**Home Range**	**SE**	**N**	**Home Range**[c]	**SE**
Spring	22	108.52	20.54	20	28.18	4.32	42	71.39 A	12.43
Summer	20	76.14	13.31	18	19.24	5.65	39[b]	50.31 AB	8.70
Winter	18	34.42	9.38	16	6.62	1.33	35[b]	21.57 B	5.34
Fall	18	68.67	13.17	16	18.12	5.32	33[b]	45.64 AB	8.75
All (composite)	25	81.26	14.12	22	19.83	3.01	47	53.30	8.78

[a] spring: 16 March to 1 June, summer: 2 June to 30 September, fall: 1 October to 15 January, winter: 16 January to 15 March

[b] Includes Fox Squirrel of unknown sex

[c] Seasons with the same letter are similar at $\alpha = 0.05$.

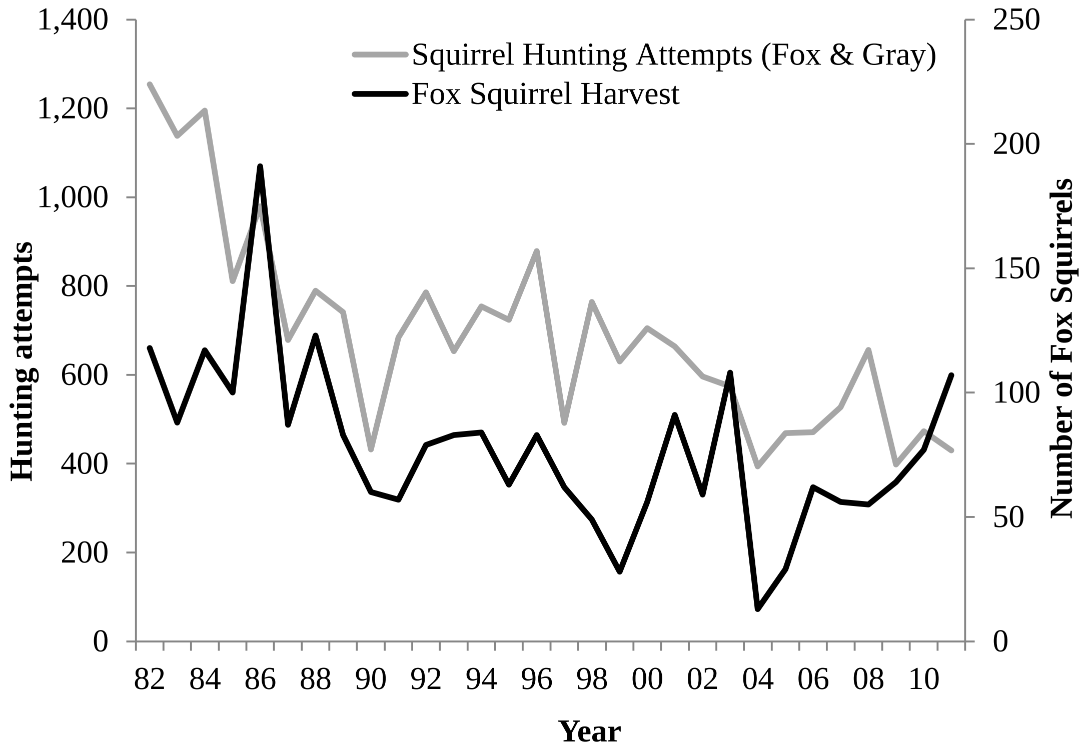

Figure 1. Southeastern Fox Squirrel and Eastern Gray Squirrel hunting attempts and Southeastern Fox Squirrel harvest on Fort Bragg, North Carolina, USA, 1982 – 2011.