

SMALL MAMMAL RESPONSE TO FOOD, FIRE, HERBICIDE AND PREDATION IN
LONGLEAF PINE ECOSYSTEM

By

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To my parents, wife and daughter

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Abstract of Thesis Presented to the Graduate School
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SMALL MAMMAL RESPONSE TO FOOD, FIRE, HERBICIDE AND PREDATION IN
LONGLeAF PINE ECOSYSTEM

By

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Little is known about demographic parameters of the southern flying squirrel (*Glaucomys volans*) or factors influencing those parameters. We conducted a capture-mark-recapture study to provide rigorous estimates of survival rates for the southern flying squirrel in a longleaf pine ecosystem. We also experimentally examined the effect of food supplementation, prescribed fire and mammalian predator exclusion on their survival rates. Apparent monthly survival was $0.84 \pm \text{SE } 0.01$, with no evidence for sex-specific or seasonal variation. Survival was higher for adults (0.85 ± 0.01) than for juveniles (0.77 ± 0.05). Prescribed fire positively influenced survival; survival increased for a period up to six months after burns. There was no evidence that food supplementation and exclusion of mammalian predators influenced survival. These results suggest that the southern flying squirrel population in our study site is not food limited and mammalian species are not the major predator for this species.

Rapid decline and degradation of longleaf pine ecosystems in southeastern United States are conservation concerns. Prescribed fire is the primary management activity in this fire-dependent ecosystem, but prescribed fire is under increasing scrutiny due to air quality issues. There are concerns that prescribed fire may be removed, or replaced by

herbicide, as a forest management tool without adequate understanding of its ecological consequences. We conducted a capture-mark-recapture study from April 1999 to April 2002 to examine experimentally the effect of prescribed fire, herbicide application and herbicide-prescribed fire combination on apparent survival rates of *Peromyscus gossypinus* and *Sigmodon hispidus* population. There was no evidence that herbicide application affected survival of cotton mice. Evidence to support effect of prescribed fire and herbicide-fire combination on survival of cotton mice was weak; apparent monthly survival increased after these treatments. There was strong evidence that prescribed fire and herbicide-fire treatments affected survival of cotton rats, but the evidence of a herbicide effect alone was weak; survival rates declined after all three treatments. Fire alone had a stronger effect than an herbicide-fire treatment in both species. A detailed study of ecological consequences of these alternative management practices should be carried out before replacing or augmenting prescribed fire with herbicide.

CHAPTER 1 INTRODUCTION

Longleaf pine (*Pinus palustris*) ecosystem is a species-rich endangered ecosystem of North America (Noss et al. 1995; Alavalapati et al. 2002). Once a dominant ecosystem in southeastern United States covering more than 36 million ha before the arrival of European settlers (Landers et al. 1995), it is now restricted to less than 1.2 million ha (Alavalapati et al. 2002). Over millennia, anthropogenic and lightning-ignited frequent fire has been dominant ecological process maintaining the longleaf pine ecosystem; disruption of these fire regimes, along with various other anthropogenic factors, is thought to be an important cause of rapid decline and degradation of this ecosystem (Van Lear et al. 2005). Longleaf pine ecosystems require some management activity to maintain the favorable grassy understory. Prescribed fire during the growing season has been the primary management activity for the maintenance or restoration of this fire-dependent ecosystem (Frost 1990; Glitzenstein et al. 1995; Streng 1993). However, prescribed fire is under increased scrutiny due to perceived air quality issues, particularly the emission of atmospheric particles and their potential impacts on human health (Sandberg et al. 2002). A possible alternative to prescribed burning involves applications of herbicide alone or in combination with prescribed fire. Besides these ecosystem level management tools, population level management activities like supplemental feeding in different form and predator exclusion or removal are also employed, primarily for the management of game birds.

Small mammal population dynamics in longleaf pine forest affected by many natural processes and anthropogenic activities. Food, fire and predation are arguably three of the most important factors affecting small mammal demography in fire

maintained habitat such as the longleaf pine ecosystem. Several studies have experimentally evaluated additive and interactive effects of food, predation and fire on demographic variables of small mammals (Krebs et al. 1995; McNamara and Houston 1987; Mitchell et al. 1992; Morris et al. 2011b; Morris et al. In press; Sinclair and Pech 1996). However, no study has tested for the population-level effects of food, fire and predation on the southern flying squirrels (*Glaucomys volans*). In fact, little is known about demography and population dynamics of the southern flying squirrel, the most widely distributed flying squirrel of North America. Similarly, we are not aware of any study that has investigated how herbicide, alone or in combination with prescribed fire, affects small mammals inhabiting longleaf pine habitats. To fill this gap in knowledge, the first chapter of this thesis investigates the survival rate of southern flying squirrel and tests for the effect of food supplementation, mammalian predator exclusion and prescribed fire on southern flying squirrel survival. The second chapter of this thesis aims to provide data on population-level impact of longleaf pine ecosystem management practices (Prescribed fire, herbicide application and herbicide-fire combination) on small mammals inhabiting the longleaf pine ecosystem ecosystem.

CHAPTER 2
THE INFLUENCE OF MAMMALIAN PREDATOR EXCLUSION, FOOD
SUPPLEMENTATION AND PRESCRIBED FIRE ON SURVIVAL OF THE SOUTHERN
FLYING SQUIRREL IN A LONGLEAF PINE ECOSYSTEM

Background

Food and predation are thought to be two of the most important factors influencing population dynamics of small mammals; every small mammal requires food to survive and is a potential prey for others. Several studies have evaluated population-level influence of experimentally-supplemented food on small mammals. These studies revealed that food supplementation can lead to a larger body size (Cole and Batzli 1978), longer breeding season (Hansen and Batzli 1979; Taitt and Krebs 1983), greater density (Hubbs and Boonstra 1997), increased survival (Ransome and Sullivan 2004), and larger litter size (Campbell and Slade 1995; Cole and Batzli 1978). However, the population-level effect of food supplementation can vary among species and habitats. For example, recent food supplementation studies (Morris et al. 2011b) in a longleaf pine (*Pinus palustris*)-wiregrass (*Aristida beyrichiana*) ecosystem showed that food supplementation increased survival, abundance and rate of transition from non-reproductive to reproductive states in the hispid cotton rat (*Sigmodon hispidus*). On the same site, Morris et al. (In press) found that supplemental food increased abundance but not survival in cotton mice (*Peromyscus gossypinus*) and oldfield mice (*P. polionotus*). Likewise, Ransome and Sullivan (1997) found that supplemental food increased population size but had no measurable influence on proportion of adults breeding, or survival or recruitment rates in northern flying squirrel (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*). However, another study with the same two species (Ransome and Sullivan 2004) revealed that survival of northern flying

squirrels was significantly higher on grids with food supplementation whereas the red squirrel population did not respond to supplemental food.

Predation plays a vital role in population dynamics of any prey species. Increase in mortality rate is the most obvious effect of predation and in small mammals the amount of activity leading to increased visibility, audibility or smell raises the predation risk (Norrdahl and Kporpimaki 1995). Predator exclusion or removal experiments led to increased densities in cotton rats and meadow voles (*Microtus pennsylvanicus*) (Schnell 1968), and survival in degu (*Octodon degus*) (Meserve et al. 1993). In southern Georgia, experimental exclusion of mammalian predators had no effect on demographic parameters of hispid cotton rat and cotton mice, but it positively influenced survival and abundance of oldfield mice (Morris et al. 2011b; Morris et al. In press).

In small mammal species inhabiting fire-maintained ecosystems, such as the longleaf pine ecosystem, frequency and scale of fire can also influence populations (Pyne et al. 1996). Fire reduced survival, abundance and/or transition from non-reproductive to reproductive states in cotton rat, cotton mice and oldfield mice (Morris et al. 2011b; Morris et al. In press); similar results were reported for northern flying squirrels in ponderosa pine (*Pinus ponderosa*) and mixed conifer forests (Lehmkuhl et al. 2006). Tree squirrels appeared to benefit indirectly from low intensity ground fires which stimulated cone and fungi production and created open stands that facilitate foraging (Weigl et al. 1989).

Several studies have experimentally evaluated additive and interactive effects of food, predation and fire on demographic variables of small mammals (Krebs et al. 1995; McNamara and Houston 1987; Mitchell et al. 1992; Morris et al. 2011b; Morris et

al. In press; Sinclair and Pech 1996). However, we know of no study that has tested for the population-level effects of food, fire and predation on the southern flying squirrel (*Glaucomys volans*). In fact, little is known about demography and population dynamics of the southern flying squirrel, the most widely distributed flying squirrel of North America. Our specific objectives were to: (1) provide rigorous estimates of survival rates, and to test for sex- and age-specific and seasonal variation in survival, and (2) experimentally test for additive and interactive effects of food supplementation, mammalian predator exclusion, and prescribed fire on survival of the southern flying squirrel.

Materials and Methods

Study Area

The study was conducted at the Joseph W. Jones Ecological Research Center at Ichauway, a 12,000 ha site managed for research, education and conservation, located in Baker County, Georgia. The site is primarily a longleaf pine and wiregrass ecosystem with associated hardwood tree species, wetlands, slash pine (*Pinus elliottii*) and a variety of other habitats (Atkinson et al. 1996). Longleaf pine-grassland ecosystem is shaped frequent fire, induced by either humans or lightning (e.g., Van Lear et al. 2005). Our study site was managed by prescribed fire (Glitzenstein et al. 1995), and the Center employed dormant and growing season burns in an approximate two-year burn rotation 4,000–6,000 ha annually.

Study Species

The southern flying squirrel is one of two species of the genus *Glaucomys*; the other is the northern flying squirrel. Its distribution ranges from temperate to sub-temperate pine-hardwood forests from southernmost Quebec southward through the

eastern half of the United States to Honduras (Dolan and Carter 1977). Flying squirrels are relatively long lived (~10 years), and use tree cavities for nut storage, defecatoria, den sites and breeding sites; individuals may use several cavities (Brady et al. 2000). They compete with other cavity nesting species, such as the red cockaded woodpecker (*Picoides borealis*), for available nest sites (Stabb et al. 1989). It is generally accepted that populations of southern flying squirrels have increased and that they are a threat for conservation of endangered red cockaded woodpeckers (Borgo et al. 2010; Werner and Peacor 2003), but little is known about population ecology of this species.

Field Methods

There were four mammalian predator exclusion plots in the Jones Center; each was surrounded by 4 ft. tall woven wire fencing with three parallel electric wires at top, middle and bottom to prevent climbing and digging by potential predators. The size of the fence weave allowed movement of small mammals and snakes in and out of the predator exclosures. Significantly fewer mammalian predators in exclosures than in control plots was evident from regular track counts and thermal camera surveys (Conner et al. 2010). When mammalian predators were detected inside exclosures, efforts were made to trap and remove them. A nearby site with same size and similar habitat was selected as a control plot for each exclosure. Size of these control and exclosure plots ranged from 36 to 49 ha. Because of their geographical proximity and habitat similarity, pairs of control and exclosure plots were considered as one site.

Supplemental food was provided by placing cans with 113 g of rabbit chow at every other station in two exclosure and two control grids from June 2007 to August 2009. These grids were randomly selected and feeding stations were checked and refilled every other week. Supplemental feeding was continued on two randomly

selected exclosures from July 2010 to November 2010 with 300 g of rolled oat. This time plastic feeders were placed 2 m high up in the tree in 4*4 grids with approximately 60 m between the stations. Feeding stations were checked and refilled every week. Motion sensitive trail cameras revealed the regular use of feeding stations by flying squirrels and other species of small mammals.

Prescribed fires were executed in Februaries of 2005, 2007 and 2009 according to the Center's burn plan.

As part of an ongoing study of small mammals, a 12×12 small mammal trapping grid was established in all 4 control and 4 exclosure sites, with about 15 m between stations. Sherman live traps (H.B Sherman Traps, Tallahassee, Florida, USA) were placed on the ground. Additionally, 24 traps (4 traps in each alternate row) were set at about 2m high on the nearest suitable tree. Grids in each plot were trapped once per season from May 2003 through June 2007, and twice per season from July 2007 through August/September 2009. Trapping was continued twice per season in one exclosure and one control from September 2009 to May 2010. The remaining 6 plots were not trapped during that time. In May 2010, 6 plots (two controls, two predator exclosures and two predator exclosures plus food supplementation) were randomly selected for a flying squirrel study. Traps, mounted on wooden platforms, were set 2 m high in the nearest suitable tree in the same 12×12 small mammal trapping grid. Trapping was done twice per season through November 2010.

During each trapping session, traps were set for 4 consecutive days (Monday - Thursday). The traps were baited with rolled oats and mixed bird feed, and checked every morning. Fire ant invasion of baited trap for small mammals is a major problem in

the southeastern United States (Mitchell et al. 1996), so we sprinkled granular insecticide (Talstar) around each trap to prevent fire ant infestation. Newly caught individuals were marked with metal ear tags in both ear and released at the capture site. For all captured individuals we recorded: date, location, identity (if previously captured), sex, mass, state (adult or juvenile based on mass), reproductive condition and hind foot length. Individuals weighing more than 50 g were classified as adult (Laves and Loeb 2006).

In June 2010, in the six plots selected for the flying squirrel study, 16 wooden nest boxes were placed in a suitable tree at about 2m high in a 4x4 grid with 60 m between the nest boxes. The internal dimensions of the nest boxes were 13x13x36 cm with 3 cm entrance hole on the side (Brady et al. 2000). Nest boxes were checked every week for the presence of flying squirrels. Squirrels in the nest boxes were captured and newly captured individuals were marked and data were collected as described previously. If a litter was found in the nest box, number, sex and mass of newborns were recorded. After recording the relevant data, squirrels were released back into the nest box.

All field methods were approved by the University of Florida Institute of Food and Agricultural Sciences Animal Research Committee and were in accordance with the recommendations of the American Society of Mammalogists (Gannon et al. 2007).

Statistical Method and Capture–Mark–Recapture (CMR) Analysis

There were 39 4-day capture occasions from May 2003 to November 2010. Each year was divided into four seasons; spring (March 20 - June 20), summer (June 21 - September 22), fall (September 23 - December 20) and winter (December 21 - March 19). Two different capture protocols (tree traps only, and ground traps with intermittent tree traps) used in this study were taken into account to investigate the effect of capture

method on capture probability. Individuals not caught in the traps but found during weekly nest box monitoring were added to the trapping dataset for that week. Because control and exclosure plots within each site share similar habitat characteristics, we also tested for a site effect on capture probability and apparent survival rate.

Models were built for program MARK version 6.1 (White and Burnham 1999) by analyzing CMR data with R version 2.12.2 (R Development Core Team 2011) package RMark 2.0.1 (Laake and Rexstad 2008). Monthly apparent survival (ϕ) and capture probability (p) were estimated and modeled using Cormack-Jolly-Seber (CJS) models. We performed a goodness of fit test using the median \hat{c} approach in program MARK (White and Burnham 1999) and found no evidence of over dispersion or lack of fit ($\hat{c} = 1.00$). Akaike's information criterion corrected for small sample size (AICc) was used for model comparison and statistical inference.

We conducted preliminary analyses to identify the best base model for p and ϕ such that treatment effects could be evaluated in subsequent analyses. The best base model for p was investigated with time dependent ϕ , taking into account the potential influence of trapping session, year, sex, capture method, season, site, and their additive and interactive effects on capture probability. The best-supported model for p was then used to investigate the best base model for ϕ taking into account the potential influence of trapping session, year, sex, season, site, and their additive and interactive effects on survival. Effects of food supplementation, predator exclusion and prescribed fire on ϕ were then sequentially added to the best base model (i.e., p (sex + capture type) ϕ (site + year)).

The effect of prescribed fire on small mammals is mainly through the changes in habitat brought about by the fire event (Smith 2000). Duration of this effect varies for different species (Morris et al. 2011b; Morris et al. In press). We tested for the different effect window of prescribed fire for southern flying squirrel by fixing the survival for all sessions except those following fire and allowing survival to vary for different length of time (3, 6 and 9 months) after the fire event. The best-supported fire effect window on survival was then added to the base model to test for the effect of fire on survival. We also tested for additive and interactive effects of all three treatments (food supplementation, predator exclusion and prescribed fire; 2-way interactions only) on survival.

Finally, we used multistate CMR models to estimate and model state-specific (adult or juvenile) apparent survival (S) and state transition probability (ψ) (Nichols et al. 1991). There was no evidence that capture probability varied between juvenile and adult squirrels; thus, we fixed p to p (sex + capture type), and tested for seasonal, annual, sex-, strata- and site-specific variation in S and ψ . Probability of transition from adult to juvenile was fixed to zero. Data limitations did not allow us to test for treatment effects using the multistate CMR model.

Results

From July 2003 to November 2010, we captured 433 individual flying squirrels 1258 times. Of these, 556 were captured from May 2003 to May 2010 (ground traps with intermittent tree traps) and 702 were captured from June 2010 to November 2010 (all tree traps). The sex ratio of captured individuals was 49.5% females and 50.5% males. Weekly nest box monitoring from June to October 2010 resulted in 59 (40

females and 19 males) individuals being captured a total of 105 times. Only two females with litters were found; with 4 and 3 offspring.

Initial investigations revealed that capture probability was best described by an additive effect of sex and capture type (ground traps vs. tree traps; Table 2-1). Capture probability was substantially higher for tree traps ($0.80 \pm \text{SE } 0.039$) than for ground traps with intermittent tree traps (0.27 ± 0.028); it was higher for females (0.59 ± 0.0359) than for males (0.33 ± 0.032).

Overall monthly apparent survival was 0.84 ± 0.011 . There was no evidence for sex-specific or seasonal variation in survival; instead, the model that included an additive effect of site and year received overwhelming support (Table 2-2). Survival varied over years in all four sites (Figure 2-1); with the higher survival at site 2 (0.88 ± 0.012) and lowest at site 4 (0.73 ± 0.04), and highest in year 2004 (0.95 ± 0.033) and lowest in year 2010 (0.72 ± 0.024).

The most parsimonious model testing for the food effect included an additive effect of food supplementation (Table 2-3a). However, the effect of food supplementation was negative, with monthly apparent survival being lower during the period of food supplementation (food: 0.67 ± 0.05 ; no food: 0.76 ± 0.03). Furthermore, the model with an additive effect of supplemental food differed from the base model only by $\Delta\text{AICc} = 1.12$, suggesting no strong evidence for the food supplementation effect on survival.

Analyses to quantify the fire effect window indicated that fire affected survival for up to 6 months following the prescribed burn (Table 2-4). There was some evidence ($\Delta\text{AICc} = 3.21$) that fire positively affected survival (Table 2-3b). Apparent monthly survival increased following burns (after fire: 0.91 ± 0.05 ; before fire: 0.74 ± 0.047)

(Figure 2-2). The base model (which did not include the effect of mammalian predator exclusion) had a lower AICc value than that for the model including the effect of mammalian predator exclusion, suggesting that exclusion of mammalian predators did not influence survival (Table 2-4c).

Next, we evaluated the additive and interactive effects of food supplementation, predator exclusion and prescribed fire. The most parsimonious model included the additive effect of fire; adding additive or interactive effect of food supplementation and predator exclusion to the base model did not improve the model parsimony (Table 2-5). However, the most parsimonious model carried only 23% model weight, suggesting substantial model selection uncertainty.

Based on multi-state CMR modeling, the apparent monthly survival was higher for adults (0.85 ± 0.01) than for juveniles (0.77 ± 0.05). The transition probability (probability of juveniles reaching an adult weight) varied seasonally, and was highest in fall (0.92 ± 0.06) and lowest in summer (0.23 ± 0.13) (Figure 2-3).

Discussion

Despite their wide geographic distribution (Dolan and Carter 1977), little is known about the population ecology of the southern flying squirrel. In fact, we were unable to find any study that reported survival or population growth rate for this species; this is surprising given its reputation as an abundant species that is considered a pest in some areas (Borgo et al. 2010; Laves and Loeb 1999). Using a CMR approach, this study was undertaken to fill the gap in knowledge, and to provide sex- and state-specific (based on age class – adult or juvenile) estimates of survival rates. Furthermore, we experimentally tested for the effect of food, fire and mammalian predators, arguably 3 of

the most important factors affecting small mammal demography, on survival of southern flying squirrels.

The overall capture probability in our study was 0.47, but it was substantially higher for tree traps compared to ground traps. Lehmkuhl et al (2006), in a study using both tree and ground traps, reported a capture probability of 0.14 for northern flying squirrels, which is substantially lower than our estimates for southern flying squirrels. We found that females were more likely to be captured than males, an observation also reported for the Siberian flying squirrel (*Pteromys volans*) (Lampila et al. 2009). High energy requirements of females during pregnancy and lactation could make food more attractive to females, resulting in increased capture probabilities in baited traps.

The overall monthly apparent survival was 0.84, but it varied both among sites and years. These variations may reflect the influence of microhabitat differences among sites and/or environmental variation. However, apparent annual survival for a close relative, the northern flying squirrel, has been reported to be 0.47 – 0.51 in eastern Washington state's Cascade Range (Lehmkuhl et al. 2006), and 0.32 – 0.68 in the northern coastal range of Oregon (Gomez et al. 2005). Likewise, average annual adult survival for Siberian flying squirrels has been reported to be 0.43-0.53 (Lampila et al. 2009). The overall annual survival (calculated from the monthly survival) for our study population was 0.12, which is substantially lower than those reported for other species of flying squirrels. The causes of the rather substantial differences in survival among flying squirrel species (particularly between northern and southern flying squirrels) remain unclear. However, it should be noted that these apparent survival estimates confound mortality and permanent immigration, and none of these studies addresses

the issue of movement. Indeed, the relatively low survival rate for the southern flying squirrels in our study site is surprising, given the widely-held belief that the southern flying squirrel populations are increasing in numbers in most of its range.

Among the three factors considered in this study (fire, food and mammalian predator exclusion), only fire was found to substantially influence survival of southern flying squirrels. Apparent monthly survival was higher for up to 6 months after the burn in all four sites during all three burn years. The positive impact of fire on arboreal flying squirrels might be due to a decreased structural complexity of understory vegetation after fire events which facilitates locomotion and increases the ability of flying squirrels to detect and avoid predators (Bendel and Gates 1987; Metcalfe 1984; Schooley et al. 1996); an increase in abundance of food due to fire-triggered growth of fungi (Fujimura et al. 2005) may also help improve survival post-fire. Dense understory vegetation due to fire suppression may force squirrels to travel long distances for foraging, thereby increasing predation risk (Pasch and Koprowski 2011). The improvement in survival for up to 6 months suggests that the benefits to survival following fire disappear after about 6 months, likely due to a progressive increase in understory vegetation. However, we do not know if the observed increase in survival due to prescribed fire in our study is specific to our study site or occurs more widely, because no other study has evaluated the response of southern flying squirrels to prescribed fire. Survival of ground-dwelling small mammals on the same study sites either showed no response (Cotton mice and oldfield mice, Morris et al. In press) or was negatively affected by prescribed fire (Cotton rat, Morris et al. 2011). These differences may have occurred because of differences in resource needs between the southern flying squirrel, an arboreal species,

and the ground-dwelling small mammals. However, analysis of annual variation in apparent monthly survival showed that survival was highest in 2004, which was a non-burn year, and lowest in 2007, which was a burn year. This probably implies that annual variation in environmental variables have greater influence than prescribed fire on the survival of the southern flying squirrel.

There was limited evidence that food supplementation affected survival; furthermore, the effect was in the opposite direction than expected in that food supplementation reduced survival. Other small mammals (cotton rats, cotton mice and oldfield mice) on the same study sites had increased survival, increased rates of transition to reproductive states and greater abundance in response to food supplementation (Morris et al. 2011; Morris et al. In press). The lack of response to supplemental food by the flying squirrels suggests that that food was not limiting southern flying squirrels during our study. Other species of squirrels have shown either no effect or only marginal effect of supplemental feeding on population parameters (Havera and Nixon 1980; Klenner and Krebs 1991; Sullivan 1990), but we know of no study reporting the negative effect of supplemental food. The decrease in flying squirrel survival could just be a coincidence, with factors other than supplemental food influencing survival during the time of supplemental feeding, or it could be due to a higher prey activity attracting predator towards the feeding stations (Boutin 1990; Turner et al. 2008).

Mammalian predator exclusion had no effect on survival of southern flying squirrels. Although mammalian mesopredators were excluded from predator exclusion sites, access to these sites by avian predators and snakes was not affected; indeed,

raptors and snakes, rather than mammalian mesocarnivores, are perhaps more important predators of these cavity-dwelling arboreal mammals (Carey et al. 1992; Laves and Loeb 1999; Mitchell et al. 1999; Rudolph et al. 1990). Scat analysis of bobcat (*Lynx rufus*) at the present study site reported < 10% of the bobcat scats contained southern flying squirrel remains (Godbois 2003); other studies have reported flying squirrel as the most common prey species for spotted owl (*Strix occidentalis*) (Carey et al. 1992; Forsman et al. 1984). Spotted owls are not present in this study site but there is plenty of barred owl (*Strix varia*) which would have similar impact like that of spotted owl. Studies have shown high use of cavity nests (Holloway and Malcolm 2007) and nest predation of various avian species by southern flying squirrel (Goertz et al. 1975; Kilham 1968; Stabb et al. 1989). To avoid larger predators (such as raccoons and bobcats), southern flying squirrels apparently prefer cavities which are not yet enlarged by other cavity users (Loeb 1993; Rudolph et al. 1990b), and this makes them especially vulnerable to snake predation as the small entrance hole restricts their escape route once the cavity is intruded by snakes.

It is intriguing that the southern flying squirrel had a lower apparent survival rate than its threatened counterpart, the northern flying squirrel considering that the former is often considered a pest species. It is well known that species characterized by early maturity and high reproductive rates have potential for rapid population growth in favorable circumstances (Oli and Dobson 1999, 2003, 2005; Pianka 1970). The ability of southern flying squirrel populations to increase rapidly may, therefore, be facilitated by high reproductive rates and/or early maturity. In fact, flying squirrels can produce more than one litter a year (Dolan and Carter 1977). A detailed study of their population

ecology is needed to understand the demographic basis and environmental effects of southern flying squirrel population dynamics.

Table 2-1. Model comparison table of top ten models for Cormack-Jolly-Seber capture-mark-recapture analysis to investigate the best base model for capture probability (p) for southern flying squirrels at Jones Ecological Research Center, Newton, Georgia from year 2003-2010. For these analyses, the apparent survival rate (ϕ) was constrained to be time specific. Table includes the number of parameters (K), Akaike's information criterion corrected for small sample size (AICc), difference in AICc (Δ AICc) and model weights (relative likelihood of models in the set).

Model no	Model	K	AICc	Δ AICc	Model weight
1	p (sex + capture type ^a)	41	1311.545	0.000	0.633
2	p (sex * capture type)	42	1313.636	2.091	0.223
3	p (sex + year)	47	1314.505	2.960	0.144
4	p (sex * year)	54	1329.731	18.186	0.000
5	p (sex + time)	77	1333.625	22.080	0.000
6	p (capture type)	40	1336.894	25.349	0.000
7	p (year)	46	1339.033	27.488	0.000
8	p (time)	76	1362.750	51.206	0.000
9	p (sex + season ^b)	43	1390.749	79.204	0.000
10	p (site ^c * season)	54	1395.881	84.336	0.000

^a capture type: Ground traps and tree traps

^b season: Winter (December 21-March 19), Spring (March 20-June 20), Summer (June 21-September 22) and Fall (September 23-December 20)

^c site: The mammalian predator exclosure plot, paired with a nearby control plots with similar habitat characteristics. Thus, there were 4 sites, each with 1 control and 1 exclosure plot.

Table 2-2. Model comparison table of top 15 model for Cormack-Jolly-Seber capture-mark-capture analysis of southern flying squirrels to investigate the best base model for survival (ϕ) in the Jones Ecological Research Center, Newton, Georgia from 2003-2010. For this analysis capture probability (p) was modeled as p (sex + capture type). See Table 1 for column definitions, and description of capture type, site, and season.

Model no	Model	K	AICc	Δ AICc	Model weight
1	ϕ (site + year)	14	1268.581	0.000	0.980
2	ϕ (site + season)	10	1276.850	8.268	0.016
3	ϕ (site * season)	19	1279.896	11.314	0.003
4	ϕ (year)	11	1285.582	17.001	0.000
5	ϕ sex + year)	12	1287.650	19.069	0.000
6	ϕ (season)	7	1288.356	19.775	0.000
7	ϕ (season * sex)	11	1290.001	21.419	0.000
8	ϕ (season + sex)	8	1290.402	21.821	0.000
9	ϕ (sex * year)	19	1290.440	21.858	0.000
10	ϕ (site * year)	35	1294.149	25.568	0.000
11	ϕ (site)	7	1307.689	39.108	0.000
12	ϕ (sex + site)	8	1309.232	40.651	0.000
13	ϕ (site * sex)	11	1310.264	41.682	0.000
14	ϕ (time)	41	1311.545	42.963	0.000
15	ϕ (sex + time)	42	1313.820	45.239	0.000

Table 2-3. Model comparison table of top four models for Cormack-Jolly-Seber capture-mark-recapture analysis of southern flying squirrels to investigate the effect of food supplementation, prescribed fire and mammalian predator exclusion on survival (ϕ) in the Jones Ecological Research Center, Newton, Georgia from 2003-2010. The best base model for ϕ was an additive effect of site and year. For these analysis capture probability (p) was modeled as p (sex + capture type). See Table 1 for column definitions and description of site and capture type.

Model no	Model	K	AICc	Δ AICc	Model weight
(a) Effect of food supplementation					
1	ϕ (site + year + food)	15	1267.460	0.000	0.606
2	ϕ (site + year)	14	1268.581	1.121	0.345
3	ϕ (site * food + year)	18	1272.571	5.111	0.047
4	ϕ (site + year * food)	22	1280.387	12.93	0.001
(b) Effect of prescribed fire					
1	ϕ (site + year + fire)	15	1265.370	0.000	0.600
2	ϕ (site * fire + year)	18	1267.720	2.355	0.185
3	ϕ (site + year)	14	1268.581	3.216	0.120
4	ϕ (site + year * fire)	18	1269.060	3.691	0.095
(c) Effect of mammalian predator exclusion					
1	ϕ (site + years)	14	1268.581	0.000	0.691
2	ϕ (site + year + predator exclusion)	15	1270.578	1.997	0.254
3	ϕ (site + year * predator exclusion)	22	1274.686	6.105	0.033
4	ϕ (site * predator exclusion + year)	18	1275.439	6.857	0.022

Table 2-4. Model comparison table for Cormack-Jolly-Seber capture-mark-recapture analysis of southern flying squirrels to investigate the best fire effect window on survival (ϕ) in the Jones Ecological Research Center, Newton, Georgia in the 2005, 2007 and 2009. For these analysis capture probability (p) was modeled as p (sex + capture type). See Table 1 for column definitions.

Model no	Model	K	AICc	Δ AICc	Model weight
1	ϕ (fire effect over the period of 6 months)	15	1265.366	0.000	0.594
2	ϕ (fire effect over the period of 3 months)	15	1266.420	1.054	0.351
3	ϕ (fire effect over period of 9 months)	15	1270.113	4.748	0.055

Table 2-5. Model comparison table of the top ten models for Cormack-Jolly-Seber capture-mark-recapture analysis of southern flying squirrels to investigate the additive and interactive effects of food supplementation, mammalian predator exclusion and prescribed fire on survival (ϕ) in the Jones Ecological Research Center, Newton, Georgia from 2003-2010. The best base model for ϕ was an additive effect of site and year. For these analysis capture probability (p) was modeled as p (sex + capture type). See Table 1 for column definitions and description of site.

Model no	Model	K	AICc	Δ AICc	Model weight
1	ϕ (site + year + fire)	15	1265.370	0.000	0.230
2	ϕ (site + year + fire + food)	16	1265.780	0.412	0.187
3	ϕ (site + year + predator exclusion + fire)	16	1267.400	2.033	0.083
4	ϕ (site + year + food)	15	1267.460	2.094	0.081
5	ϕ (site + year + predator exclusion * fire)	17	1267.480	2.115	0.080
6	ϕ (site + year + fire * food)	17	1267.660	2.296	0.073
7	ϕ (site + year + predator exclusion + food + fire)	17	1267.860	2.495	0.066
8	ϕ (site + year + predator exclusion * fire + food)	18	1268.580	3.212	0.046
9	ϕ (site + year)	14	1268.580	3.216	0.046
10	ϕ (site + year + predator exclusion + food)	16	1269.540	4.172	0.029

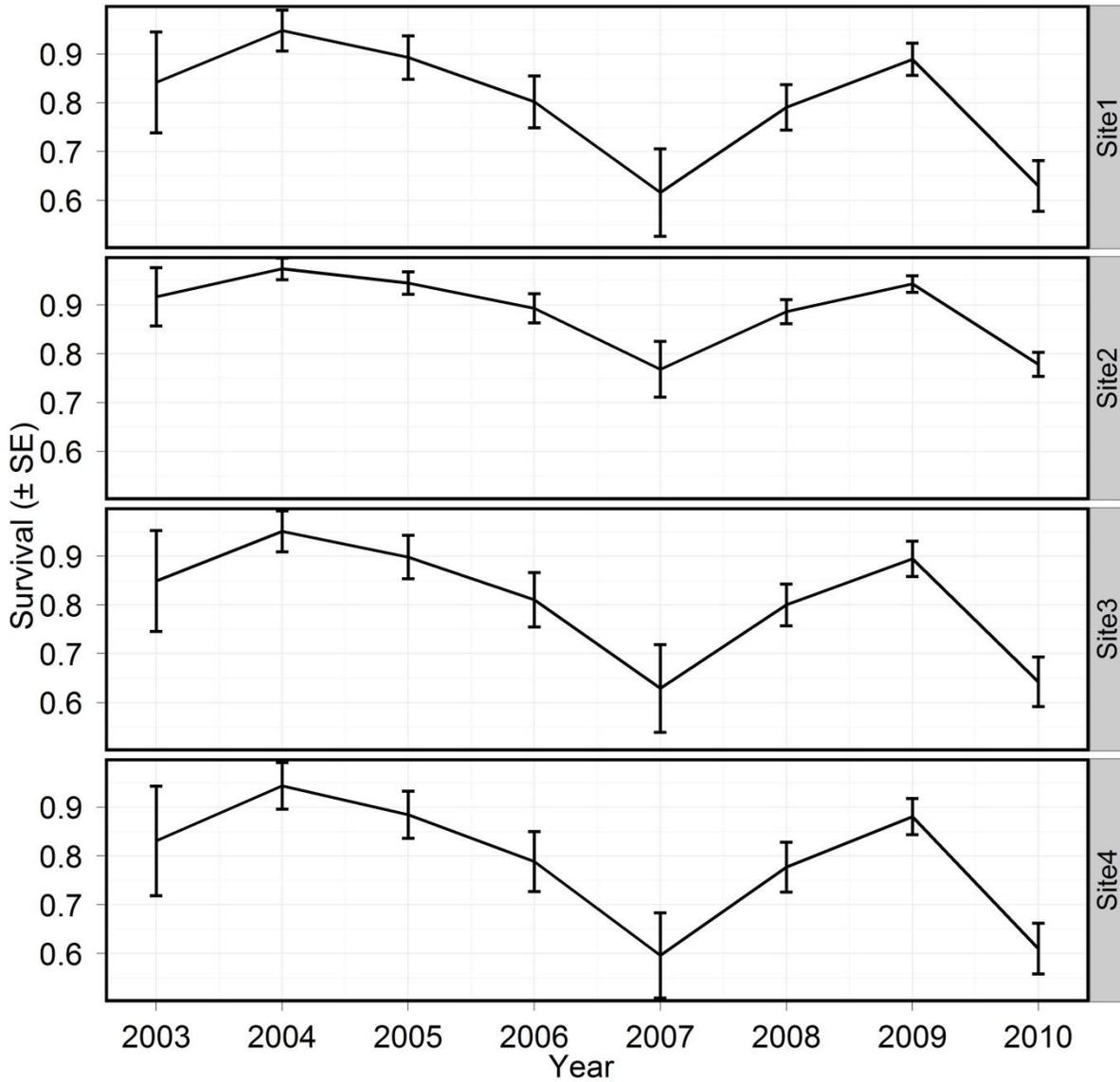


Figure 2-1. Monthly apparent survival estimates (\pm SE) of southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia at four sites from 2003-2010. Survival was modeled with additive effects of site and year. The mammalian predator exclosure plot, paired with a nearby control plot with similar habitat characteristics constitutes a site.

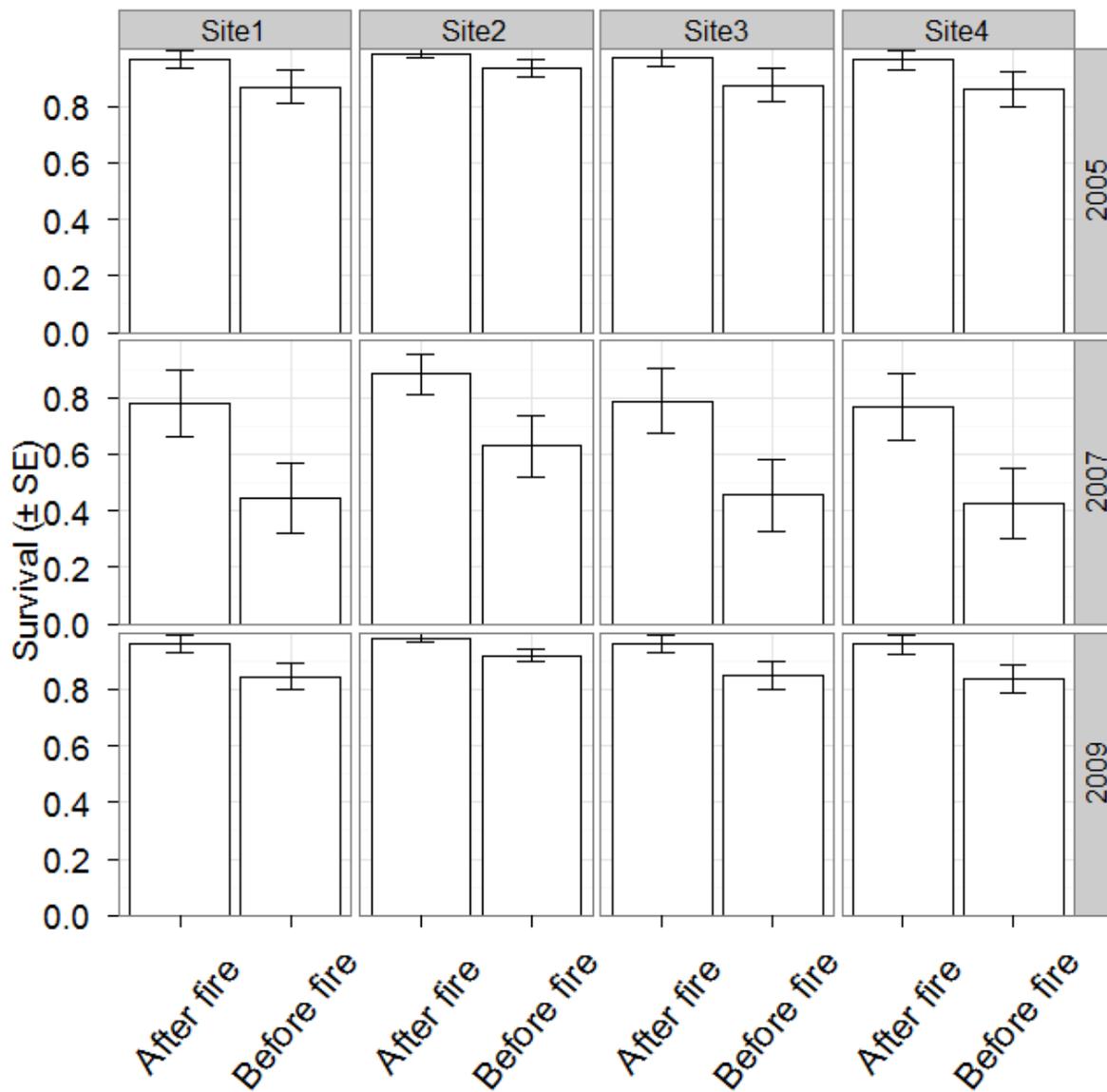


Figure 2-2. Comparison of monthly apparent survival estimates (\pm SE) of southern flying squirrels before and 6 months following prescribed fire at four sites in the Jones Ecological Research Center, Newton, Georgia during three years of prescribed fire (2005, 2007 and 2009). The effect of fire is modeled as an additive effect to the base model for survival (site + year). The mammalian predator exclosure plot, paired with a nearby control plot with similar habitat characteristics constitutes a site.

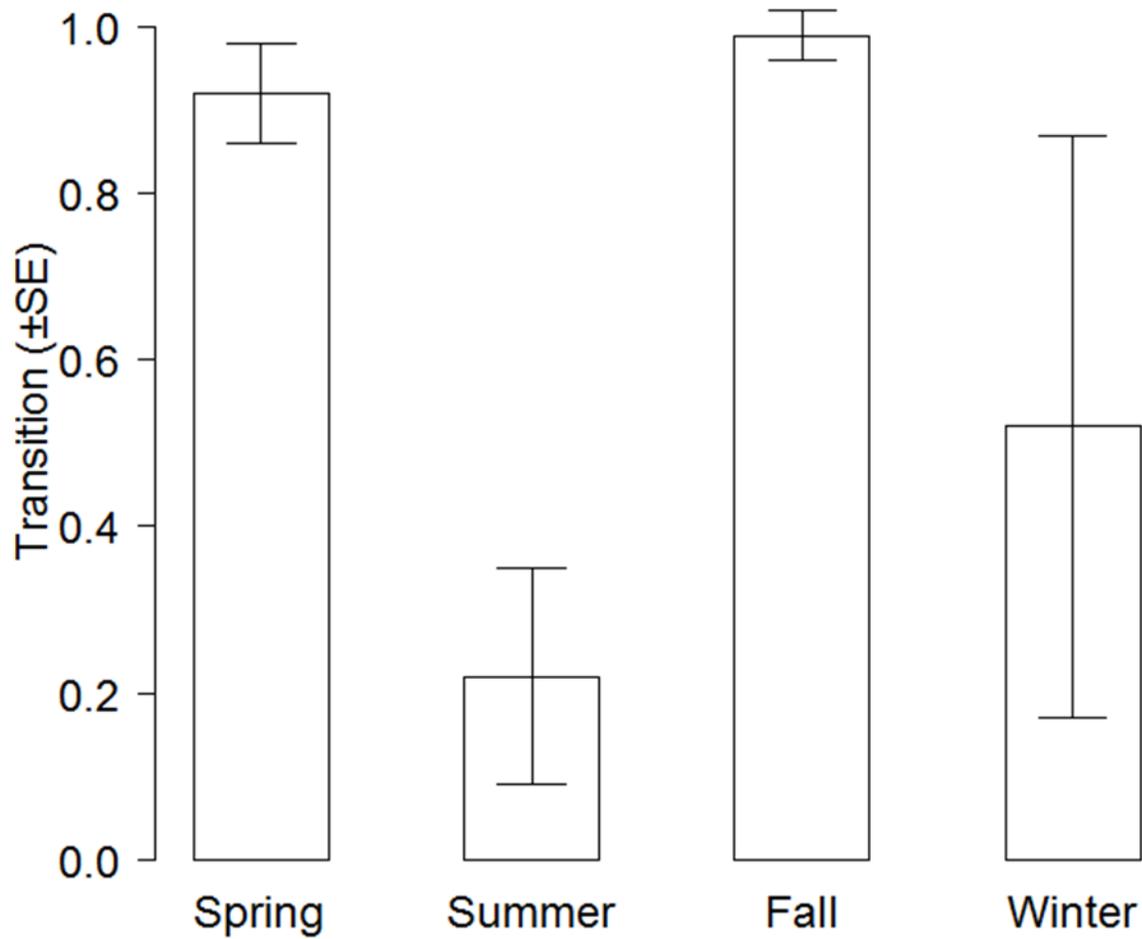


Figure 2-3. Seasonal variation in transition probability (\pm SE) from juvenile to adult state for southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia from 2003-2010. Individuals weighing less than 50 g were classified as juveniles.

CHAPTER 3 LONGLEAF PINE MANAGEMENT PRACTICES AND THEIR IMPACT ON SMALL MAMMAL POPULATIONS

Background

The longleaf pine (*Pinus palustris*) ecosystem once covered more than 36 million ha before the arrival of European settlers (Landers et al. 1995). This ecosystem has now been restricted to less than 1.2 million ha and is listed as critically endangered (Noss et al. 1995). Over millennia, anthropogenic and lightning-ignited frequent fire has been a dominant ecological process maintaining the longleaf pine ecosystem; disruption of natural fire regimes, along with other anthropogenic factors, is thought to have been an important cause of the rapid loss and degradation of the longleaf pine ecosystem (Van Lear et al. 2005). Rich biological diversity of longleaf pine ecosystem supports hundreds of floral and faunal species (Alavalapati et al. 2002); more than 30 of these, including some notable species like gopher tortoise (*Gopherus polyphemus*) and red-cockaded woodpecker (*Picoides borealis*) are now listed as either threatened or endangered (Landers et al. 1995). About 14% of mammal species inhabiting the longleaf pine ecosystem are identified as species of conservation concern (Engstrom et al. 2001). Loss and degradation of this ecosystem is a serious threat to the long term persistence of many obligate species (Brockway et al. 2005).

Prescribed fire during the growing season has been the primary management activity for the maintenance or restoration of this fire-dependent ecosystem (Frost 1990; Glitzenstein et al. 1995; Streng 1993). Every year, 10⁶ ha of forestlands are subjected to prescribed fire in the southeastern United States to maintain native ground cover vegetation and to control encroachment of hardwood (Cain et al. 1998; Richter et al. 1982). However, prescribed fire is under increased scrutiny due to perceived air quality

issues, particularly the emission of atmospheric particles and their potential impacts on human health (Sandberg et al. 2002). A possible alternative to prescribed burning involves applications of herbicide alone or in combination with prescribed fire. Herbicide application, followed by prescribed fire, has been suggested to be more effective in restoring the longleaf pine ecosystem than the use of prescribed fire alone (Brockway and Outcalt 2000). The use of herbicide for modifying wildlife habitats and for invasive plant control has increased in commercial pine plantation of southern United States (Miller and Miller 2004). There are concerns that prescribed fire may be removed, or replaced by herbicide, as a forest management tool without adequate understanding of ecological consequences of replacing (or augmenting) prescribed fire by herbicide.

The population level response of small mammals to prescribed fire is fairly well understood (Arata 1959; Conner et al. 2011; Landers 1987; Morris et al. In press; Morris et al. 2011), but I am not aware of any study that has investigated the effect of herbicide, alone or in combination with prescribed fire, on small mammals inhabiting longleaf pine habitats. To fill this gap in knowledge, my goal was to provide data on population-level impact of aforementioned longleaf pine ecosystem management practices on small mammals inhabiting the longleaf pine ecosystem. Specifically, I aimed to test experimentally whether and to what extent survival of cotton rat (*Sigmodon hispidus*) and cotton mice (*Peromyscus gossypinus*) was affected by herbicide, prescribed fire and the combination of the two.

Materials and Methods

Study Area

This study was conducted at the Joseph W. Jones Ecological Research Center in Baker county, Georgia. This 12,000 ha site is located on the upper coastal plain and is managed for research, education and conservation. This is primarily a longleaf pine and wiregrass (*Arista stricta*) ecosystem with associated hardwood tree species, wetlands, slash pine and a variety of other habitats (Atkinson et al. 1996).

Study Species

Cotton mice are one of the most common and abundant semi-arboreal small mammals of pine forests in southeastern United States (Clark and Durden 2002). The semi arboreal nature of this species makes sparse mat of grass, abundant woody materials and logs, and short over story an important microhabitat component (Mengak and Guynn 2003).

Cotton rats are also abundant across the southeastern United States. These solitary, crepuscular rodents occur in many habitats, but require thick a cover of dense grasses, herbs and shrubs for food and cover (Goertz 1964).

Field Methods

This study was conducted at four different sites within the Jones Ecological Research Center from April 1999 to April 2002. Each site, known as burn units, was divided into 3 plots with each plot receiving 1 of 3 treatments; 1) prescribed fire alone, 2) herbicide application, followed by prescribed fire, and 3) herbicide application alone. A total of 12 treatment plots (3 treatment × 4 replicates) was established. Size of each treatment plots was ≥8 ha; most were considerably larger because the plots were delineated using existing roads and firebreaks.

Small mammal trap stations were placed along 3 systematically located transects within each plot. Ten trap stations were placed on each transect with 15 m between stations, and at each station two Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida, USA) were placed approximately 1 m apart. During each trapping session, traps were set for four consecutive days. The traps were baited with rolled oats. Each captured small mammal was identified to species, weighed, sexed and released at the capture site. Cotton rats were marked individually with ear tags on both ears, and cotton mice were marked by toe clipping. Grids in each site were trapped every two months from April 1999 through November 2001, and after an interval of five months in April 2002.

Herbicide was applied in February 2000 when vegetation was just beginning to leaf out. Hexazinone herbicide (Velpar^R L, DuPont) was applied as spot treatment using backpack sprayers and metered spot gun applicators to achieve a rate of 2.5 to 3 quarts per acre. Application of prescribed fire was delayed due to draught conditions in spring but burns were successfully carried out in June 2000. All field methods followed recommendations of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Statistical Method and Capture-Mark-Recapture (CMR) Analysis

There were 17 4-day capture occasions from April 1999 to April 2002. Each year was divided into four calendar seasons; spring (March 20 - June 20), summer (June 21 - September 22), fall (September 23 - December 20) and winter (December 21 - March 19).

Monthly apparent survival (S), capture probability (p) and transition probability (ψ) from juvenile to adult were estimated and modeled using multistate CMR models

(Nichols et al. 1992; Williams et al. 2002). Cotton rats weighing > 50 g (Bergstrom and Rose 2004) and cotton mice weighing > 19 g (Bigler and Jenkins 1975) were classified as adults. Models were built for program MARK version 6.1 (White and Burnham 1999) with R package RMark 2.13.0 (R Development Core Team 2011; Laake and Rexstad 2008). Goodness of fit tests using the median \hat{c} approach in program MARK provided no evidence for lack of fit for either species (cotton mice: $\hat{c} = 0.997$; cotton rat: $\hat{c} = 0.969$). Akaike's information criterion corrected for small sample size (AICc) was used for model comparison and statistical inferences (Burnham and Anderson 2002; Williams et al. 2002).

Preliminary analyses were conducted to identify appropriate base models for S , p and ψ such that treatment effect could then be added in the subsequent analyses. For all these analyses, transition from adult to juvenile was fixed to zero because such transitions are not biologically plausible. The base model for p was investigated with time dependent S and ψ , taking into account the potential influence of trapping session, year, sex, seasons, site, state and their additive and interactive effects on p . The resulting best-supported model for p , along with time dependent ψ , was then used to investigate the base model for S , taking into account the potential influence of factors that could potentially affect survival rate; trapping session, year, sex, season, site, state, and additive and interactive effects of site and year. Finally, the base model for p and S were used to investigate the appropriate base model for ψ , taking into account the effect of trapping session, year, sex, season and site.

Changes in cover and food resources brought about by prescribed fire, herbicide application, and their combination, can last for months; thus, effects of these treatments

could influence cotton mice and cotton rat survival for varied amounts of time (Morris et al. 2011a; Morris et al. 2011b). Thus, we first investigated the best effect window for each of these treatments on survival of both species, using the base models identified in preceding analyses. For each treatment, we investigated three different effect windows (2, 4 and 6 months). As each of our study plots had either one of the three treatments applied, we used three categories of capture intervals: control (periods of time and sites when none of the treatments were in effect); treatment (sites where the given treatment was in effect for the treatment window in question); and other (periods of time and sites when the other two treatments could have been in effect, set with a broad window: June 2000 - December 2000). Survival for all “control” intervals was fixed and survival rate were allowed to vary for 2, 4 and 6 months of time following treatment in that particular treatment plot. The best supported effect window for three different treatments were compared with base models that contained no treatment effect.

Results

Cotton Mice

From April 1999 to April 2002, we captured 1083 individual cotton mice 3206 times. The sex ratio of captured individuals was slightly biased towards males (55.7%) than females (44.3%). Initial investigations revealed that cotton mice capture probability was best described when modeled with an additive effect of sex and capture occasion; monthly apparent survival best described when modeled with an interactive effect of site and year; and probability of transition from juvenile to adult when modeled with annual variation in this parameter (Table 3-1).

Overall monthly apparent survival was $0.78 \pm SE 0.01$. There was no evidence for sex-specific or state-specific variation in survival. However, apparent monthly survival of

male (0.79 ± 0.01) was slightly higher than of female (0.77 ± 0.01), and survival of adult (0.79 ± 0.01) was slightly higher than that of juveniles (0.73 ± 0.03). Monthly apparent probability of transition from juvenile to adult was 0.83 ± 0.05 .

Analysis to investigate best effect window for different treatments did not reveal strong support for any particular effect window (Table 3-2). We selected the top ranked model for further analyses: survival effect of fire lasting up to 2 months after fire event; that of herbicide lasting up to 2 months following herbicide application; and the survival effect of herbicide application, followed by fire lasting up to 6 months (Table 3-2).

There was no evidence that herbicide application affected cotton mice survival. Fire, and a combination of herbicide and fire increased apparent monthly survival of cotton mice (Figure 3-1), but the evidence for this effect was weak (Table 3-3).

Cotton Rat

From April 1999 to April 2002, we captured 969 individual cotton rats 2218 times. The sex ratio of captured individuals was even with 51% female and 49% males. Initial analysis revealed that cotton rat capture probability was best described when modeled with seasonal variation in this parameter; apparent monthly survival best described when modeled with time specific variation in this parameter; and transition probability from adult to juvenile best described when modeled with sex specific variation in this parameter (Table 3-4). Time dependent survival indicates that survival varies for each capture occasion, and this model was not helpful for testing for treatment effects. Also, herbicide and fire treatments were applied at two different seasons, and season and treatment effects could have been confounded. Thus we selected the top ranked model that did not include season and time effects (i.e., S (site + years)) as base model for testing treatment effects.

Overall apparent monthly survival was 0.67 ± 0.01 . There was no evidence for sex-specific or state-specific variation in survival. Probability of transition from juvenile to adult was 0.91 ± 0.04 .

Analysis to investigate best effect window for different treatments did not reveal strong support for any particular effect window. We selected the top ranked model for further analysis: survival effect of fire lasting up to 6 months after fire event; that of herbicide lasting up to 6 months following herbicide application; and survival effect of herbicide application followed by fire lasting up to 6 months (Table 3-5).

There was strong evidence that prescribed fire and herbicide application followed by fire affected cotton rat survival but the evidence for effect of herbicide application on survival was weak (Table 3-6). The apparent monthly survival rate declined after the prescribed fire, herbicide application and herbicide-fire combination (Figure 3-2). The effect of fire alone was stronger than fire executed after herbicide spray.

Discussion

Longleaf pine ecosystems are among the most biologically diverse habitats and harbor many species of conservation concern (Alavalapati et al. 2002; Landers et al. 1995). This ecologically important ecosystem is being lost to various anthropogenic activities at a rapid rate, and much of the remaining longleaf pine forests are seriously degraded due primarily to suppression of fire that historically maintained understory vegetation and kept hardwood encroachment at bay. Prescribed fire is a primary tool for the restoration of longleaf pine ecosystem but various factors associated with expanding human settlement and economic constraint is increasingly limiting its application (Van Lear et al. 2005). Herbicide application, alone or in combination with fire, has been suggested as an alternative to prescribed fire. Studies investigating the ecological effect

of herbicide application in pine forest of southeastern United States are lacking and I sought to quantify effects of fire and herbicide treatments, alone and in combination, on survival of two widely distributed rodents in southeastern United State.

Although the effect of prescribed fire and herbicide–fire combination on survival of cotton mice population was weak, these treatments were associated with an increase in cotton mice survival. Increase in local availability of food resources brought about by fire in the southeastern United States could be beneficial for cotton mice (Sharp et al. 2009) and this could have increased the survival rate after fire events. Since the support for effect of these two treatments on survival of cotton mice was so weak, observed increase in survival rate could just be a coincidence, with other factors influencing survival. A study in longleaf pine stands in Georgia (Morris et al. In press), stream terrace hardwood stands in Louisiana (Blanchard 1991; Goatcher 1990) and Gulf Coastal plain of south-central Alabama (Sharp et al. 2009) revealed that prescribed fire did not have significant influence on the survival of cotton mice population. Greater versatility in refuge selection and preference for underground sites like stump holes and gopher tortoise (*Gopherus polyphemus*) burrows as refuge (Frank and Layne 1992) makes cotton mice less susceptible to direct effects of fire as well as the potential increase in mortality due to reduced vegetative cover after fire (Derrick et al. 2010).

In contrast, there was evidence that fire, herbicide and herbicide followed by fire substantially reduced monthly survival of cotton rats. This was expected because cotton rats are highly susceptible to predation by different species of raptors, mammalian predators and snakes (Conner et al. 2011), and require heavy vegetative cover to avoid predation. Other studies have also shown that survival rate of cotton rats in longleaf

pine ecosystem declined after prescribed fire, primarily due to increased predation (Bock and Bock 1978; Conner et al. 2011; Morris et al. 2011) but we could not find any study reporting the survival effect of herbicide and herbicide – fire combination in cotton rat population. Positive effect of increased local availability of food on survival rate as observed in cotton mice was missing in cotton rat. However, Rehmeier et al (2005) reported that, in the long run, fire application could be beneficial due to increase in local availability of food. This suggests that for cotton rats, changes in habitat brought by fire event would be detrimental due to increased predation risk in the short run but in the long run increased abundance in local availability food resources may be beneficial. Though all three treatments affected survival in the same direction, their strength differed, with prescribed fire having the strongest effect and herbicide application the weakest. The reasons behind these differences are unclear. I hypothesize that underlying differences in ecological processes brought about by these treatments had varied levels of influence upon the survival rate of cotton rats. A clear understanding of whether or not the herbicide and herbicide-fire combination would have same beneficial effect in the long run as been reported with fire will require further study.

Two species of small mammals with different natural history responded differently to different longleaf pine management practices. Prescribed fire had opposite effects in these two species although for both species the strength of the fire effect declined in response to prior herbicide application. There was some evidence for effect of herbicide application on survival of cotton rat but not on cotton mice. It is possible that even though herbicide alone may mimic some of the ecological effects of fire, it fails to reproduce the same ecological processes as the fire and the application of herbicide

prior to fire. Herbicide reduces understory vegetation but unlike fire cannot replace other ecological functions such as stimulating flowering and enhancing germination of many fire-dependent species that characterize the longleaf ecosystem (Brennan et al. 1998). Restoration of the longleaf pine ecosystem is not only about restoring the structure and function of the ecosystem but also the ecological processes. Various management practices for the restoration of longleaf pine ecosystem bring about different changes in ecological processes such that they have varied influences on the population dynamics of species inhabiting it. Management activities to restore structure, function and diversity of longleaf pine come with the potential risk for some species of special interest (Van Lear et al. 2005). Long term studies are needed to evaluate the effects of management practices on other species of mammals, birds and reptiles to better understand the broader ecological impacts of these management practices. Without clear understanding of these, no other management practice should be employed as an alternative to prescribed fire.

Table 3-1. Model comparison table for multi-state capture-mark-recapture analysis to investigate base model for capture probability (p), survival rate (S) and transition (juvenile to adult) probability (ψ) for cotton mice at Jones Ecological Research Center, Newton, Georgia from year 1999 to 2002. Table includes the number of parameters (K), Akaike's information criterion corrected for small sample size ($AICc$), difference in $AICc$ ($\Delta AICc$) and model weights (relative likelihood of models in the set). Only top 5 models are shown for each variable.

Model No	Model	K	$AICc$	$\Delta AICc$	Model weight
Capture probability (p)					
1	p (sex + time)	49	2857.685	0.000	1.000
2	p (season ^a)	36	2877.717	20.032	0.000
3	p (season * sex)	40	2884.881	27.196	0.000
4	p (.)	33	2899.125	41.440	0.000
5	p (year)	35	2900.794	43.109	0.000
Survival (S)					
1	S (site ^b * year)	45	2843.865	0.000	0.923
2	S (site + year)	39	2849.857	5.991	0.046
3	S (year)	36	2850.708	6.843	0.030
4	S (season)	37	2858.708	14.842	0.001
5	S (site)	37	2867.724	23.858	0.000
Transition (ψ)					
1	ψ (year)	32	2811.428	0.000	0.798
2	ψ (site)	33	2814.782	3.354	0.149
3	ψ (.)	30	2818.078	6.650	0.029
4	ψ (sex)	31	2819.790	8.362	0.012
5	ψ (season)	33	2819.822	8.394	0.012

^a season: Winter (December 21-March 19), Spring (March 20-June 20), Summer (June 21-September 22) and Fall (September 23-December 20).

^b site: Four different burn units within the Jones center.

Note: Individuals weighing more than 19 g were classified as adults.

Table 3-2. Model comparison table of multistate capture-mark-recapture analysis of cotton mice to investigate the effect window of prescribed fire, herbicide application and herbicide-fire combination on survival (S) in Jones Ecological Research Center, Newton, Georgia in the year 2000. Effect windows of fire, herbicide and combined treatment was added to the base model for survival S (site * year), capture probability was modeled as p (sex + time) and transition (juvenile to adult) probability was modeled as ψ (year). See table 1 for column definitions.

Model No	Model	K	AICc	Δ AICc	Model weight
Fire effect window					
1	S (fire effect up to 2 months)	34	2810.666	0.000	0.499
2	S (fire effect up to 4 months)	34	2811.198	0.531	0.381
3	S (fire effect up to 6 months)	34	2813.513	2.847	0.120
Herbicide effect window					
1	S (herbicide effect up to 2 months)	34	2810.155	0.000	0.524
2	S (herbicide effect up to 6 months)	34	2811.732	1.577	0.238
3	S (herbicide effect up to 4 months)	34	2811.737	1.582	0.238
Combined effect window					
1	S(effect up to 6 months)	34	2810.914	0.000	0.623
2	S (effect up to 2 months)	34	2812.713	1.780	0.253
3	S (effect up to 4 months)	34	2814.163	3.250	0.123

Table 3-3. Model comparison table for multistate capture-mark-recapture analysis of cotton mice to investigate effect of prescribed fire, herbicide application and herbicide-fire combination on survival (S) in Jones Ecological Research Center, Newton, Georgia in year 2000. The base model for S was interactive effect of site and year. For these analysis capture probability was modeled as p (sex + time) and transition (juvenile-adult) probability was modeled as ψ (year). See table 1 for column definitions and description of site.

Model No	Model	K	AICc	Δ AICc	Model weight
Effect of prescribed fire					
1	S ((site * year) + fire)	34	2810.666	0.000	0.719
2	S ((site * year) + no treatment)	33	2812.544	1.877	0.281
Effect of herbicide					
1	S ((site * year) + no treatment)	33	2809.658	0.000	0.562
2	S ((site * year) + herbicide)	34	2810.155	0.497	0.438
Effect of combined treatment					
1	S ((site * year) + combined treatment)	34	2810.914	0.000	0.691
2	S ((site * year) + no treatment)	33	2812.526	1.612	0.309

Table 3-4. Model comparison table for multi-state capture-mark-recapture analysis to investigate base model for capture probability (p), survival rate (S) and transition (juvenile to adult) probability (ψ) for cotton rat at Jones Ecological Research Center, Newton, Georgia from year 1999 to 2002. See table 1 for column definitions, description of site, season, and classification of adult and juvenile. Only top 5 models are shown for each variable.

Model No	Model	K	AICc	Δ AICc	Model Weight
Capture probability (p)					
1	p (season)	36	1665.190	0.000	0.972
2	p (.)	33	1673.116	7.926	0.018
3	p (sex)	34	1674.893	9.703	0.008
4	p (site)	37	1678.178	12.988	0.001
Survival (S)					
1	S (time)	36	1665.190	0.000	1.000
2	S (season)	24	1701.667	36.477	0.000
3	S (site + year)	26	1717.285	52.095	0.000
4	S (year)	23	1719.939	54.749	0.000
5	S (site)	24	1721.549	56.360	0.000
Transition (ψ)					
1	ψ (sex)	22	1638.486	0.000	0.654
2	ψ (year + sex)	21	1640.942	2.456	0.192
3	ψ (season + sex)	23	1641.950	3.464	0.116
4	ψ (.)	24	1645.314	6.829	0.022
5	ψ (year)	24	1645.782	7.297	0.017

Note: Only four models of capture probability were able to estimate all parameters of interest.

Table 3-5. Model comparison table of multistate capture-mark-recapture analysis of cotton rat to investigate the effect window of prescribed fire, herbicide application and herbicide-fire combination on survival (S) in Jones Ecological Research Center, Newton, Georgia in the year 2000. Effect windows of fire, herbicide and combined treatment was added to the base model for survival S (site + year), capture probability was modeled as p (season) and transition (juvenile to adult) probability as modeled as ψ (sex). See table 1 for column definitions.

Model No	Model	K	AICc	Δ AICc	Model weight
Fire effect window					
1	S (fire effect up to 6 month)	14	1673.031	0.000	0.971
2	S (fire effect up to 4 month)	14	1680.144	7.113	0.028
3	S (fire effect up to 2 month)	14	1686.941	13.910	0.001
Herbicide effect window					
1	S (herbicide effect up to 6 month)	14	1691.231	0.000	0.551
2	S (herbicide effect up to 2 month)	14	1693.031	1.800	0.224
3	S (herbicide effect up to 4 month)	14	1693.031	1.800	0.224
Combined effect window					
1	S (effect up to 6 month)	14	1676.264	0.000	0.551
2	S (effect up to 4 month)	14	1676.743	0.479	0.434
3	S (effect up to 2 month)	14	1683.476	7.211	0.015

Table 3-6. Model comparison table of multistate capture-mark-recapture analysis of cotton rat to investigate effect of prescribed fire, herbicide spray and herbicide-fire combination on survival (S) in Jones Ecological Research Center, Newton, Georgia in year 2000. The base model for S was additive effect of site and time. For these analysis capture probability was modeled as p (seasons) and transition (juvenile-adult) probability was modeled as ψ (sex). See table 1 for column definitions and description of site.

Model No	Model	K	AICc	Δ AICc	Model weight
Effect of prescribed fire					
1	S (site + year + fire)	14	1673.031	0.000	0.749
2	S (site + time + no treatment)	13	1690.837	17.806	0.000
Effect of herbicide					
1	S (site + time + herbicide)	14	1691.231	0.000	0.303
2	S (site + year + no treatment)	13	1692.683	1.452	0.147
Effect of combined treatment					
1	S (site + time + combined treatment)	14	1676.264	0.000	0.500
2	S (site + time + no treatment)	13	1684.116	7.851	0.010

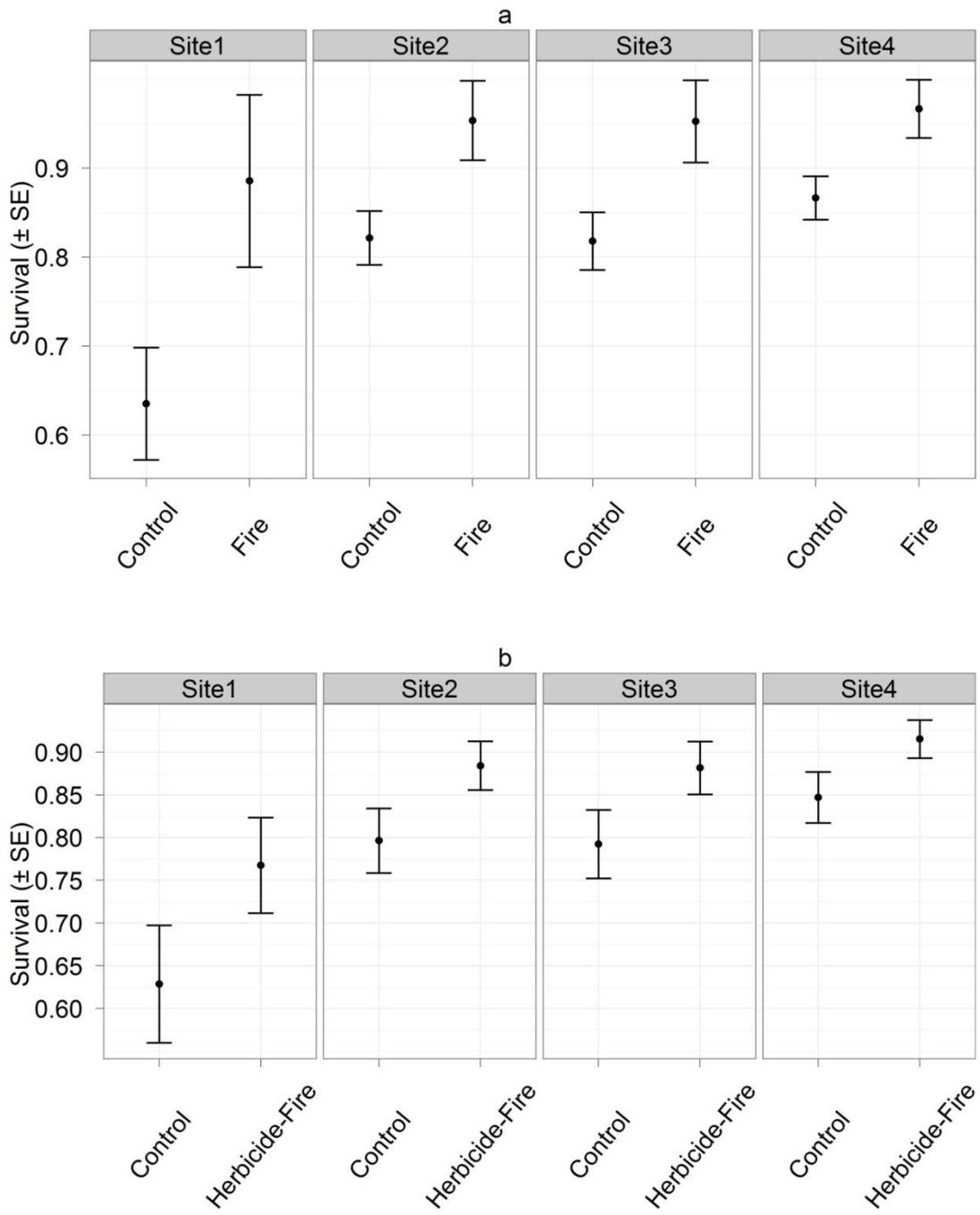


Figure 3-1. Effect of prescribed fire (a) and herbicide – fire combination (b) on monthly apparent survival (\pm SE) of cotton mice at Jones Ecological Research Center, Newton, Georgia in the year 2000. Sites are four areas within the center selected for the study.

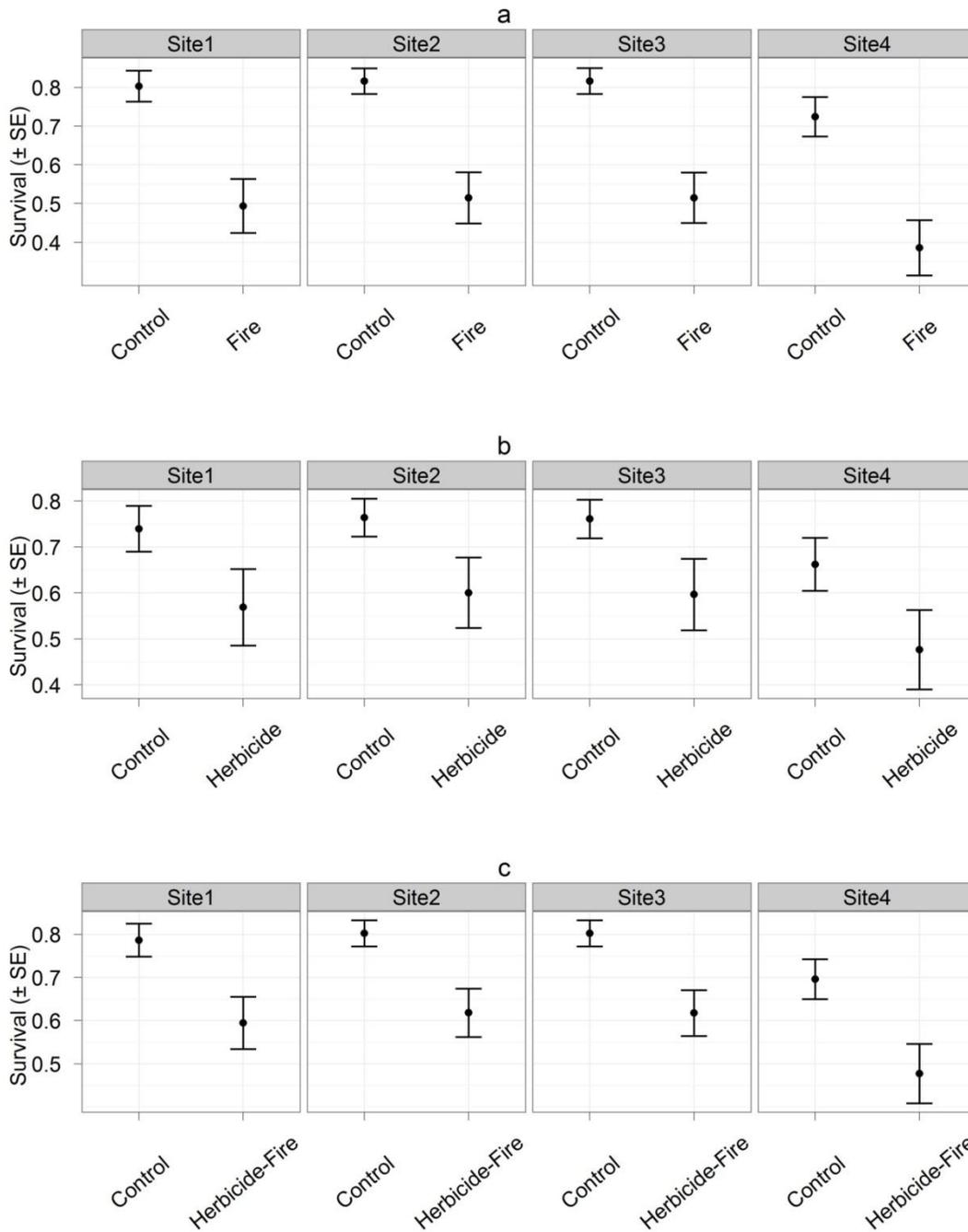


Figure 3-2. Effect of prescribed fire (a), herbicide application (b) and herbicide – fire combination (c) on monthly apparent survival estimates (± SE) of cotton rat at Jones Ecological Research Center, Newton, Georgia in the year 2000. Sites are four areas within the center selected for the study.

CHAPTER 4 CONCLUSIONS

Long leaf pine ecosystem is regarded as one of the most treasured forest ecosystem of southeastern United States which supports hundreds of floral and faunal species (Noss et al. 1995; Alavalapati et al. 2002). Over millennia, anthropogenic and lightning-ignited frequent fire has been a dominant ecological process maintaining the longleaf pine ecosystem. Various factors have contributed to the decline and degradation of this endangered ecosystem since European colonization. This rapid decline and degradation of longleaf pine ecosystem is a conservation concern. Prescribed fire during the growing season has been the primary management activity for the maintenance or restoration of this fire-dependent ecosystem (Frost 1990; Glitzenstein et al. 1995; Streng 1993). But this practice is under increased scrutiny due to perceived air quality issues. There are concerns that prescribed fire may be removed, or replaced by herbicide, as a forest management tool without adequate understanding of ecological consequences of replacing (or augmenting) prescribed fire by herbicide. Beside these ecosystem levels management tools, population level management tools like food and exclusion of predator are also commonly employed for game bird management. The objective of this study was to evaluate the effect of these management practices on the population dynamics of small mammals inhabiting longleaf habitat.

Prescribed fire which at present is a primary management activity for the restoration of longleaf ecosystem also was the most important factor influencing the population dynamics of small mammal species inhabiting longleaf pine ecosystem. However, different species of small mammals responded differently to fire event.

Prescribed fire positively influenced survival rate of cotton mice and southern flying squirrels whereas prescribed fire's influence on the survival rates of cotton rats was negative. The changes in vegetation brought about by fire event were beneficial for the flying squirrel and cotton mice but detrimental to cotton rat. There was no effect of herbicide alone on survival rate of cotton mice but herbicide- fire combination increased the survival rate. Both herbicide alone and herbicide-fire combination decreased the survival of cotton rat. We observed that ecological effect of herbicide and herbicide- fire combination was weaker than that of fire alone. The populations of flying squirrel in our study system were not limited by food resources and mammalian species are not a major predator for this arboreal flying squirrel in our study system.

Various management practices for the restoration of longleaf pine ecosystem bring about different changes in ecological processes such that they have varied influences on the population dynamics of species inhabiting it. This study suggests that herbicide could not mimic all the ecological function of fire and we do not suggest replacing prescribed fire with other management tools without clear understanding of their ecological consequences.

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BIOGRAPHICAL SKETCH

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