

DEMOGRAPHY OF SMALL MAMMAL POPULATIONS IN LONGLEAF PINE  
UNDERGOING RESTORATION

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DEMOGRAPHY OF SMALL MAMMAL POPULATIONS IN LONGLEAF PINE  
UNDERGOING RESTORATION

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THESIS ABSTRACT

DEMOGRAPHY OF SMALL MAMMAL POPULATIONS IN LONGLEAF PINE  
UNDERGOING RESTORATION

Nicholas Wingate Sharp

Master of Science, May 13, 2005  
(B.S., University of Alabama in Huntsville, 2001)  
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Successfully restoring the ecosystem function of a small mammal community, as part of a holistic ecosystem restoration effort, requires focus on population dynamics that operate over multiple spatial scales. I participated in a replicated, manipulative experiment investigating the use of fire and fire alternatives to restore a longleaf pine ecosystem, formerly one of the most expansive and biologically diverse ecosystems of North America. I conducted a four-year mark-recapture study, comprising 119,700 trap nights, to assess demographic responses of small mammal populations to habitat alteration. Survival of golden mice (*Ochrotomys nuttalli*) was affected negatively by fire. Survival and recruitment of cotton mice (*Peromyscus gossypinus*) were affected differently by restoration efforts. Survival varied over three spatial scales. Recruitment responded to both on-site habitat alteration and availability of immigrants from source habitat outside restoration areas. Attempting to restore historic assemblages of animal

communities requires assessment of changes in population demographics as they respond to habitat alteration at a local scale, within the context of the surrounding landscape.

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Style manual or journals used: Ecological Applications, Journal of Mammalogy

Computer software used: Microsoft Office 2003, Program MARK 4.1, SAS 8.2,

SigmaPlot 9.0

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## INTRODUCTION

Humans have been contending with fire in the longleaf pine forests of southeastern North America since they arrived on the continent. The first European visitors to the region encountered vast expanses of sparsely distributed longleaf pine with an open understory of grasses and forbs (Platt 1999)<sup>a</sup>. In this region where almost daily summer thunderstorms cause one of the highest concentrations of lightning strikes in the world, fire was a natural and regular occurrence. Because of its commercial importance, mainly as a source for naval stores, longleaf pine was the first tree species of North America to be studied in detail (Frost 1993). Studies of fire in longleaf pine followed (e.g., Hayward 1939<sup>b</sup>, Wahlenberg et al. 1939<sup>c</sup>). Despite a long history of fire studies, surprisingly little is known about the effects of fire on the small mammal community of the longleaf pine ecosystem.

Boyer (1964) is the only researcher to document the small mammal community of longleaf pine stands in Alabama. Komarek (1939), Arata (1959), and Layne (1974) reported the effects of fire on the small mammal community in longleaf pine stands. Additionally, Shadowen (1963), Hatchell (1964), Hofstetter 1973), and Layne (1974) demonstrated an increase in the numbers of cotton mice captured after fire in southern pine forests. None of these studies were of adequate sample sizes or experimental designs to infer mechanisms that caused the observed changes. Although there have been few studies of the effects of fire on the small mammals of longleaf pine, there have been many studies of the effects of habitat manipulation on the small mammal community in a

wide range of vegetation communities (Ahlgren 1966, Beck and Vogl 1972), Sullivan and Sullivan 1982, Masters et al. 1998). These studies included the effects of fire, herbicide, mechanical alteration, or some combination thereof. Unfortunately, most of these studies still failed to link changes in habitat to changes in the vital rates of species (but see McMurry et al. 1996). Such a link is required if the effects of treatments, or more generally, habitat quality, are to be accurately assessed.

I studied the effects of fire and fire alternatives on the small mammal community living in longleaf pine stands in which the natural process of fire has been interrupted. The study took place at Auburn University's Solon Dixon Forestry Education Center (Dixon Center) in south-central Alabama. This research was part of the Fire and Fire Surrogate Study (FFS), a joint effort between the US Department of the Interior and the US Department of Agriculture to identify effective methods for restoring the United States' fire-maintained ecosystems. I had three objectives, 1) determine the desired future condition of the small mammal community so that I could set goals for restoration and judge the effectiveness of restoration treatments, 2) determine if restoration treatments affected small mammals, and 3) link demographic rates of cotton mice (*Peromyscus gossypinus*) to habitat defined at a local and landscape scale.

Fieldwork had already begun when I joined the project in the summer of 2002. The experimental design and the trapping protocol had already been established. The decision to follow Pollock's robust design was particularly wise, as it provided several advantages in the data analysis. I identified the need to develop a picture of the small mammal community living in a fire-maintained savanna and initiated trapping in Conecuh National Forest (Conecuh NF). Realizing that the trapping schedule missed the

breeding season entirely, I began trapping in the winter in hopes of collecting information about reproduction and juvenile survival. The addition of trapping in Conecuh NF and in the winter greatly expanded my insights, and improved data analysis in ways I had not foreseen.

To meet my objectives I conducted a capture-recapture study of the small mammals living at the Dixon Center and in Conecuh NF. In Chapter 1, I present a detailed study of the cotton mouse population living on experimental units at the Dixon Center. I tracked changes in survival and recruitment and compared competing models to evaluate variation in these rates over time, space, and treatment. I incorporated measures of available source habitat for cotton mice to infer immigration from outside the study area.

In Chapter 2, I broadened my perspective to consider the small mammal community. I described differences between the small mammal communities living in hardwood-pine woodlands at the Dixon Center and a longleaf pine savanna in Conecuh NF. I evaluated the effects of restoration treatments on golden mice and calculated survival rates for cotton mice living in Conecuh NF, for comparison with those of mice living at the Dixon Center.

<sup>a</sup> Except for the following, literature citations appear in Chapters 1 and 2.

<sup>b</sup> Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests.

Ecology 20:287-304.

<sup>c</sup> Wahlenberg, W. G., S. W. Greene, and H. R. Reed. Effects of fire and cattle grazing on longleaf pine lands, as studied at McNeill, Mississippi. United States Department of Agriculture Technical Bulletin No. 683.

RH: Demographics of cotton mice in longleaf pine

SURVIVAL AND RECRUITMENT OF COTTON MICE IN LONGLEAF PINE  
UNDERGOING RESTORATION

**Abstract:** Decades of fire suppression policy have led to an annual epidemic of catastrophic forest fires across the United States. The Fire and Fire Surrogate study sought to determine the most ecologically and economically efficient methods to reduce fuel levels and restore ecosystem integrity in the nation's fire-maintained ecosystems, through a national network of research locations. Each location employed four replicated treatments representing options for forest restoration: 1) control - no action was taken; 2) burn - prescribed fire was used to reduce fuel levels and maintain a frequent fire regime; 3) thin - trees were removed to reduce tree density; 4) thin/burn - thinning was followed by prescribed fire. At the Gulf Coastal Plain site, where longleaf pine is the fire-maintained ecosystem being restored, I conducted a capture-recapture study and used Pollock's robust design to follow changes in the survival and recruitment of cotton mice living on experimental units. I compared competing models to evaluate variation in survival and recruitment over time, space, and treatment. I incorporated measures of available source habitat for cotton mice with reverse time modeling to infer immigration from outside the study area. The top ranked survival model contained only variation over time, but the closely ranked second and third models included variation over space and treatment, respectively. The top four recruitment models all included effects for availability of source habitat and treatment effects. I concluded treatments affected both

survival and recruitment. Burning alone appeared to create habitat sinks, while treatments combining fire with thinning or herbicide appeared to improve habitat quality. Source habitat outside the study area provided immigrants to experimental units. Results indicated that treatments might have been more effective had they been implemented over a larger area, mimicking the fires that once burned over great expanses of longleaf pine savanna.

**Key words:** capture-recapture, demography, ecosystem restoration, fire, longleaf pine, *Peromyscus gossypinus*, small mammals, survival, recruitment, robust design, reverse time

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Catastrophic wildfire, the unforeseen result of decades of fire suppression policy, has caused the loss of life and millions of dollars in property damage, destroyed vast expanses of the nation's parks and forests, and costs millions more each year to fight. The problem is now receiving attention as foresters and land managers look for ways to efficiently and safely reduce dangerous fuel levels in the nation's forests. These efforts will inevitably affect the wildlife living within the forests. If fuel reduction efforts are to be applied in an ecologically sound way, we must understand how these applications affect wildlife.

Understanding how management actions affect animal populations requires monitoring the vital rates that drive population growth. Traditionally, the goal of wildlife management has been to achieve some desired population size, or density, and monitoring efforts have focused on that demographic. Van Horne (1983) and Pulliam (1988) demonstrated density is not necessarily an accurate indicator of habitat quality,

therefore the vital rates that determine changes in population size must be considered.

Capture-recapture techniques provide robust estimates of these rates through a variety of models (e.g., Williams 2002). The ability to incorporate environmental variables as covariates in capture-recapture modeling provides an opportunity to link demographic estimation with another growing and important discipline – landscape ecology.

My research is part of the national Fire/Fire Surrogate (FFS) study, a collaborative effort between the US Department of the Interior and the US Department of Agriculture (Weatherspoon and McIver 2000). The goal of the FFS study is to determine the most ecologically and economically efficient methods to reduce fuel levels and restore ecosystem integrity in the nation's fire-maintained ecosystems. The key to achieving this goal is the implementation of an experimental design common to a nationwide network of research locations. The FFS study employed four treatments representing options for forest restoration: 1) control - no action was taken; 2) burn - prescribed fire was used to reduce fuel levels and maintain a frequent fire regime; 3) thin - trees were removed to reduce tree density; 4) thin/burn - thinning was followed by prescribed fire. All treatments are replicated three times. These treatments were intended to result in a common desired future condition (DFC) - a forest stand structure and fuel level such that 80 % of the trees would be able to survive a wildfire in all but extremely unfavorable weather conditions.

I measured the effects of experimental treatments on small mammals at the Gulf Coastal Plain site of the FFS study. The study took place at Auburn University's Solon Dixon Forestry Education Center (Dixon Center) in south-central Alabama, where longleaf pine (*Pinus palustris*) savanna is the fire-maintained ecosystem being restored.

The Dixon Center includes 2,130 ha of managed pine forestland. Sites selected for experimental units were longleaf pine stands in which the natural process of fire has been interrupted; hardwoods have grown into the canopy alongside the dominate longleaf pine and at the time of selection had a dense shrub understory dominated by yaupon (*Ilex vomitoria*). The Study Plan for the Gulf Coastal Plain site further defines the DFC as a stand structure like that of the longleaf pine savannas that once expanded across southeastern North America (Frost 1993): an open canopy dominated by longleaf pine trees and an understory of grasses and forbs with some shrubs (Outcalt 2002). Herbicide is commonly used in pine plantations of the southeast to reduce understory vegetation that would compete with pine trees, and could help achieve the understory of grasses and forbs specified by the DFC. At the Gulf Coastal Plain site a fifth treatment was added to the four FFS treatments; herbicide/burn - herbicide is applied to the shrubby understory followed by prescribed fire.

Early explorers to North America described expansive savannas featuring an open grass/forb understory and sparsely distributed longleaf pines forming open canopies (Platt 1999). The longleaf pine ecosystem supports a high diversity of plant species, making it one of the most species-rich communities outside of the tropics (Peet and Allard 1993). It is also home to the threatened gopher tortoise (*Gopherus polyphemus*) and indigo snake (*Drymarchon corais*), and the endangered red cockaded woodpecker (*Picoides borealis*).

The pyrogenic grasses and other fire-tolerant plants of the longleaf pine ecosystem evolved under a process of frequent fires ignited by the lightning strikes of spring storms. Landers et al. (1990) estimated that these fires had to occur every 2-4 years to maintain the ecosystem. These fires would burn at low intensity, sometimes over

great distances, through the continuous grass understory (Frost 1993; Peet and Allard 1993). When fire is suppressed longleaf pine savannas succeed to hardwood forests. Fuel loads build in the woody understory, which can lead to high intensity, crown-scorching wildfires (Peet and Allard 1993). Interruption of the natural fire regime, as well as conversion of longleaf pine stands for agriculture and timber plantations, has caused the loss of this expansive, unique, and species-rich ecosystem. Today longleaf pine occupies < 3% of its original range (Platt 1999).

I chose the cotton mouse (*Peromyscus gossypinus*) as a study subject because they were present in all 15 experimental units, were readily captured, and were present in large enough numbers to confidently estimate demographic variables. I also chose cotton mice because their reported affinity for bottomland hardwood forests (Wolfe and Linzey 1977) allowed me to easily map potential source habitat (Pulliam 1988) for incorporation into my demographic analysis. Cotton mice are omnivores and habitat generalists, but their optimal habitat is purported to be bottomland hardwood forests, swamps, and mesic or hydric hammocks (bottomland hardwoods; Wolfe and Linzey 1977). This assertion has never been supported with demographic data other than abundance.

Four studies of fire in southern pinelands demonstrated an increase in the number of cotton mice captured after fire (Shadowen 1963, Hatchell 1964, Hofstetter 1973, Layne 1974). None were of adequate sample size or experimental design to infer mechanisms that cause this response. Layne (1974) suggested that a rapid increase in the density of cotton mice was due to a population overload of cotton mice spilling into the burned habitat, or perhaps due to increased availability of pine and other seeds and insects on the burned area.

I expected the study treatments to affect components of the habitat that provide food and shelter for cotton mice. Prescribed fire was intended to mimic the natural process of wildfire, removing woody understory vegetation and allowing the herb layer to flourish, creating an open understory. Fire effects vegetation in several ways that should benefit cotton mice. Soft mast and seed production increase after fire (Van Lear and Harlow 2000), grasses and forbs expand coverage of the forest floor (Brockway and Outcalt 2000), and resprouting vegetation is more nutritious and palatable (Stransky and Harlow 1981). The goal of thinning was to restore stands to a density and composition resembling that of fire-maintained stands by removing deciduous trees and an overabundance of longleaf pine. I expected this would open the forest canopy and more light would reach the understory, allowing the shrub or herb layer to flourish. Garlon (Dow AgroSciences, Indianapolis, Indiana), which was used in this experiment, targets woody vegetation but is safe against grasses. Brockway and Outcalt (2000) suggested herbicide application might be a way to expedite the restoration of longleaf pine habitat by encouraging the spread of grasses and forbs while permanently removing competition from oaks and other invading woody vegetation.

I expected treatment effects on local availability of resources to create source/sink dynamics (Van Horne 1983, Pulliam 1988), altering animal dispersal patterns. A source is a habitat in which reproduction exceeds mortality. It is self-maintaining. A source produces a surplus of individuals that emigrate from the habitat. Since excess individuals are exported, density in sources is usually constant over several generations. A sink is any habitat in which reproduction is not sufficient to replace individuals lost to mortality. A population can be maintained in a sink only by immigration of surplus individuals from

a source. Density in sinks may fluctuate widely and may even be greater than that of sources. The matrix of sources and sinks across the landscape determines the probability that any one area receives immigrants.

My goal was to create a complete picture of changes in cotton mouse population demographics over the course of the study so I could evaluate whether the treatments affected cotton mice. I perceived three ways in which the processes of survival and recruitment could vary: temporally, spatially, and by treatment. I used a mark-recapture study and Pollock's robust design (Pollock 1982, Kendall et al. 1995) to estimate apparent survival (survival and emigration) and abundance. The robust design is the preferred model for estimation using mark-recapture data because it provides the most precise, theoretically substantiated, estimates of survival and capture probabilities available (Williams et al. 2002).

I estimated recruitment (births and immigration) with an asymmetric reverse time approach under multistate robust design modeling. Analyzing capture-recapture data in reverse time provides inference about the recruitment process (Pollock et al. 1974). The reverse time equivalent of survival is the seniority parameter, the probability that an animal was in the population at time  $i-1$  given that it was caught at time  $i$  (Pradel 1996). Recruitment is equal to  $1 - \text{seniority}$ . Seniority can also be interpreted as indicating the relative contributions of survival and recruitment to the population growth rate (Nichols et al. 2000). I took a novel approach to infer the immigration of individuals from outside the study area by incorporating measures of available source habitat for cotton mice in recruitment models. I evaluated hypotheses by using program MARK (White and

Burnham 1999) to compare competing models that incorporated temporal, spatial, and treatment variation in estimates of survival or recruitment.

I hypothesized that the burn, thin/burn, and herbicide/burn treatments would improve habitat for cotton mice by increasing local availability of resources, with the thin/burn treatment causing the best improvement. I hypothesized that the thin treatment alone would not affect components of the habitat that are important to cotton mice, therefore the habitat quality of thin units would be similar to that of control units. Since cotton mice are omnivores and habitat generalists, I hypothesized they would be able to locate adequate resources to survive and reproduce on thin and control units. I also hypothesized that bottomland hardwoods in close proximity to experimental units would serve as sources, providing immigrants to those units and obscuring the effects of treatments on population size. Based on my hypotheses, I predicted that: 1) population growth, survival, and recruitment would be highest on thin/burn units, followed by burn and herbicide/burn units, 2) population growth, survival, and recruitment on thin units would differ little from that of control units, the size of populations on thin and control units would not change dramatically from the beginning to the end of the experiment, and 3) recruitment would be higher in populations close to large areas of bottomland hardwoods and swamps.

## **METHODS**

### **Study area**

The Dixon Center is located in Covington and Escambia counties in the Gulf Coastal Plain of south-central Alabama (31°9' N, 086°42' W). Summers in this region are hot and humid (often 35° C and 95% humidity), while winters are mild. Average

annual precipitation is 14.22 cm (Outcalt 2002). Most precipitation occurs during late winter through spring and during afternoon showers in the summer. The terrain is relatively flat with rolling hills and ranges in elevation from 30 m to 100 m (Outcalt 2002).

Longleaf pine dominates much of the managed forest of the Dixon Center, but loblolly, slash, shortleaf (*P. echinata*), and spruce pine (*P. glabra*) are also abundant (Fischer and Holler 1990). Hardwoods can be found interspersed throughout the overstory and midstory in mixed pine-hardwood stands and concentrated along bottomland streams. Laurel oak (*Q. laurifolia*), white oak (*Q. alba*), and water oak (*Q. nigra*) are most numerous, while American beech (*Fagus grandifolia*), sweetgum (*Liquidambar styraciflua*), hickory (*Carya* spp.), maple (*Acer* spp.), ash (*Fraxinus* spp.), and elm (*Ulmus* spp.) also occur (Fischer and Holler 1990). The understory at the Dixon Center is dominated by yaupon, along with lesser amounts of blueberries (*Vaccinium* spp.) and gallberry (*I. glabra*; Outcalt 2002). In places yaupon forms shrubby thickets that are quite dense.

### **Experimental design**

The experiment was laid out in a randomized block design, with three replicates per treatment (Figure 1). Experimental units were forest stands approximately 15.2 ha in size. Three blocks were arranged so that experimental units shared similar soil types and generally shared the same location. Each of the four treatments and a control were randomly assigned to one of five experimental units within each block for a total of 15 experimental units. Minimum distance between experimental units was 156 m.

### **Treatment and trapping schedule**

All thinning took place between February and April 2002 (Figure 2). Burn and thin/burn sites were burned for the first time in April and May 2002. Herbicide was applied in September 2002. Herbicide/burn sites were burned in the spring of 2003. A second burning of the burn and thin/burn sites was conducted in the spring of 2004. Due to weather conditions, one burn site was not burned a second time until July, after the first trapping period of the summer had taken place. Trapping followed Pollock's (1982) robust design. I conducted ten trapping sessions (primary periods), each comprising seven consecutive nights of trapping (secondary periods; Figure 2). I trapped on each experimental unit twice during the summer for the four year duration of the study, with approximately one month between the two summer periods. I began winter trapping in February 2003 to gather more demographic data during the breeding season.

### **Small mammal trapping**

I sampled the small mammal community using standard capture-recapture methods. I installed a 0.81 ha trapping grid on each unit, locating most trapping grids in the center of each experimental unit. In some cases I opted to offset grids so as to avoid dirt roads. I recorded the location of trapping grids with a handheld GPS unit. Each grid had 100 trapping stations, located at the intersection of 10 rows and 10 columns placed at 10 m intervals. I placed a single Sherman live trap, baited with sunflower seeds, at each trap station. I checked traps each morning. During the summer, I closed traps during the heat of the day and re-opened and baited them in the evening. During the winter, I placed batting in each trap for nesting material. Due to time constraints imposed by short winter days, I re-baited traps and left them open during the day.

I gave each newly captured animal a uniquely numbered ear tag (monel ear tags from Western Tag Co., Salt Lake City, Utah) and recorded the sex, age (sub-adult or adult, determined by pelage *sensu* Pournelle 1952), reproductive condition (evidence of lactation in females, distended scrotum in males), weight, hind foot length, tail length, capture location, and identification number of each captured individual. I released animals at the point of capture.

### **Model selection and inference**

Model selection and inference followed the methodology of Burnham and Anderson (2002). I ranked models using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ; Akaike 1973). The model with the lowest  $AIC_c$  value is considered the most parsimonious approximation of truth among the set of candidate models, given the data. I used model deviance, the difference in  $AIC_c$  values between the top ranked model and each competing model ( $\Delta AIC_c$ ), and normalized  $AIC_c$  values (Akaike weights,  $w_i$ ) to compare the relative performance of competing models. Akaike weights can be viewed as the weight of evidence in favor of a particular model. The ratio of Akaike weights ( $w_i/w_j$ ), or evidence ratio, indicates the likelihood of one model over another (Burnham and Anderson 2002).

### **Survival models**

I used the robust design model in program MARK (White and Burnham 1999) to examine the temporal and spatial structure of survival and to evaluate the effects of the treatments on survival. I defined the nine intervals between primary periods were defined in monthly units (e.g., 45 days = 1.5 month) so that survival would be estimated as a monthly rate. Each of the 15 experimental units was treated as a separate group. The

robust design in program MARK estimates apparent survival, temporary emigration, initial capture probability, and recapture probability. I used a logit transformation (Cooch and White 2004) to incorporate characteristics of individuals (individual covariates), such as age, with estimation of survival rates. I used the Huggins estimator (Huggins 1989, 1991) to incorporate individual covariates with capture and recapture probabilities. The Huggins estimator does not include population size in the estimating equation. Population size estimates are derived from the estimated capture probabilities.

Typically, model selection begins with a goodness of fit test to ensure a highly parameterized, global model adequately fits the data. Selection proceeds with identification of models that explain the data more parsimoniously than the global model. The global model should include all effects thought to be relevant to the parameter to be estimated (Burnham and Anderson 2002). Presently, no suitable goodness of fit test exists for the robust design. Data were generally too sparse to support highly parameterized models of survival including interaction terms, so my most highly parameterized survival model approximated the effects of time, space, treatments, and age with additive model terms.

To determine the temporal structure of survival that best described the data, I fit models that estimated survival rates seasonally and periodically. For seasonal structure (*season*), I defined the intervals between primary periods as spring, summer, or fall-winter, according to the time of year between primary periods, and calculated one estimate of survival for each of the three seasons. For periodic survival (*period*) I estimated a unique survival rate for each of the nine intervals between primary periods. I also included a model in which survival rates did not vary over time.

To determine the spatial structure of survival that best described the data, I fit models that estimated survival on four spatial scales. First, I assumed each experimental unit hosts a distinct population. I presumed estimates of survival reflect local availability of resources (including competition among individuals), and therefore the population on each experimental unit should have a different survival rate. I modeled this by including an effect term for each unit (*unit*). Second, I defined a population as a group of interbreeding individuals. Using the greatest distance dispersed by a cotton mouse that has been reported, 853m (Wolfe and Linzey 1977), I used ArcGIS 8.3 (ESRI 2004) to place a 900 m buffer around each trapping grid, and dissolved these buffers into one another at points where they intersected. From this 900 m spatial configuration, I designated five neighborhoods (*neighborhood*; Figure 1). Alternatively, I considered a more localized configuration in which unit 15 was distinct from units 12, 13, and 14 (and all other groups were the same as before). This latter organization occurs at a maximum buffer distance of 570 m and constitutes the third spatial configuration (*locale*). Finally, to model the population as continuous across the study area, I included models with no spatial variation in survival estimates.

I modeled treatments in three ways: 1) I handled each treatment as a separate effect on survival (*trt*), 2) I constrained survival rates on thin units to be equal to those of control units, while the three other treatments were distinguished (*thin=control*), and 3) I constrained all units that were burned to have equal survival rates, while survival rates on thin units were equal to those of control units (*burn*). Because this later model only employs one term for the treatment effect, it was possible to model an interaction between time and treatment (*period\*burn*) without creating an over-parameterized model.

For all models, I constrained estimates of survival to be equal across all sites for the pre-treatment trapping periods.

I added each of the four parameterizations of space and each of the three parameterizations of treatment effects to the *period*, *season* and null construction of time. I also constructed models that included only temporal variation in survival. I presumed treatments caused differential survival between neighboring units, so I did not add terms grouping units in space to treatment models. The only spatial term I included in treatment models was the individual unit term. By including this term I presumed there was within-treatment variation between the three replicates. These combinations of time, space, and treatment in model structure constituted my a priori set of candidate models.

I used the same model structure of temporary emigration, capture, and recapture probabilities for all models. Given the average home range of a cotton mouse is 0.5 ha and the average life span is  $\leq 5$  months (Wolfe and Linzey 1977), I judged it unlikely an animal caught during primary period  $i$ , would emigrate from the trapping area, be unavailable for capture during period  $i+1$ , survive and return to the trapping area to be available for capture during period  $i+2$  (Kendall et al. 1995). Therefore, I set the probability of an individual temporarily emigrating from the sampling grid between primary periods to be equal to zero.

I could not calculate unique capture and recapture probabilities for each secondary period, because the size of my data set exceeded the computational capacity of program MARK. Instead, I calculated only one probability of capture and one probability of recapture for each unit for each primary period. A general, time varying model of capture probabilities such as this is appropriate for estimating population size

(Burnham and Anderson 2002). I modeled a trap response within primary periods by setting recapture probabilities equal to initial capture probabilities plus an additive behavioral response. I defined previous capture history with a dummy variable indicating whether the individual had been caught in the previous primary period and used this covariate to model a trap response across primary periods.

Inclusion of individual covariates in models requires program MARK to retrieve values from the capture history of each individual, which can be unacceptably slow for a large number of individuals. Therefore, I adopted a two-step model selection process. First, I ran my a priori set of candidate models of survival without any individual covariates. From these models I chose all those with a  $\Delta\text{AIC}_c \leq 7$ , added age as a covariate with survival, added age, sex, and previous capture history as covariates with capture probabilities, and re-ran the models.  $\Delta\text{AIC}_c \leq 7$  is a conservative cut-off point (Burnham and Anderson 2002), insuring the best approximating model was included in the second generation of models. I drew conclusions from the results of this second generation of models.

### **Recruitment models**

Pradel (1996) showed that a recruitment analysis could be performed by reversing the order of the capture histories and performing a survival analysis. His sampling design includes only one opportunity to recapture or re-sight an individual per sampling occasion. To perform a recruitment analysis in the robust design, which has multiple opportunities for recapture (secondary periods) per sampling session (primary period), I reversed the order of the primary periods while retaining the forward time order of the secondary periods. I believe that the secondary periods are asymmetrical regarding time

and that proper estimation of capture probabilities over secondary periods requires a forward time analysis. I followed the example of Nichols et al. (2002), using multistate modeling to separate age classes into states – adults and sub-adults. The robust design multistate models in program MARK integrate multistate modeling developed by Brownie et al. (1993) and Hestbeck et al. (1991) with the full likelihood robust design model of Kendall et al. (1995). The model calculates survival, initial capture probability, and recapture probability for each state, as well as the probability of transitioning from one state to the other or remaining in the same state. The closed robust design multistate model removes temporary emigration from the likelihood. I modeled differences in capture probabilities among animals with an additive behavioral response within primary periods and by using the Huggins estimator to include individual covariates in the estimation of capture probabilities.

Models of seniority resembled the survival models. I implemented the *period* time structure for seniority (the best structure of time for survival). I could not implement the unit\*time interaction for capture probabilities due to computational limitations of program MARK. Therefore, I used unit as an additive effect on time. I modeled a behavioral response to trapping between and within the primary periods as described for survival models. I only modeled a behavioral response across primary periods for the adult state (sub-adults have no previous capture history). I did not include sex as an individual covariate with capture probabilities because it caused program MARK to be unable to estimate some parameters.

Because sub-adults could not have been in the population during the previous primary period, I set the seniority probability for sub-adults to be zero. There were not

enough captures of sub-adults to calculate separate capture rates for all periods and separate transition rates for all intervals. I constrained sub-adult capture and recapture probabilities to be equal for all July primary periods and June of 2004. I estimated separate transition probabilities for each of the spring intervals; all other intervals were constrained to have the same estimate for transition probability.

I implemented treatment models in the same manner as I did with the survival models. I replaced spatial terms used in survival modeling with unit specific measures of the total area of bottomland hardwoods within 900 m and average distance to all bottomland hardwoods within 900 m. Using ArcGIS, I mapped the 15 trapping grids and all bottomland hardwoods within the study area (Figure 1). The Alabama Gap Analysis Project provided a xx m resolution map layer of bottomland hardwoods and swamps, created from National Wetlands Inventory maps and National Land Cover Data. I placed a 900 m buffer around each trapping grid and within each buffer summed the total area of bottomland hardwoods and calculated the average distance to the trapping grid from all map cells containing bottomland hardwoods. For entry into program MARK, I standardized these values by subtracting the mean of all values and dividing by the standard deviation.

## Population size and growth

For each experimental unit I calculated a time-averaged rate of population growth ( $\lambda$ ; Caswell 2001) for the 3-year span of the study, using the following formula:

$$\lambda = e^{\frac{(\log N_t - \log N_0)}{t}}$$

where  $t = 3$  (time span of three years),  $N_t$  = population size from the last period of the study (period 10), and  $N_0$  = the population size at the same time of year as period 10, three years previous, before treatment (period 2). Estimates of population size were taken from the selected best model of survival from program MARK.

## RESULTS

Over 105,000 trap nights I captured 1,190 cotton mice 5,028 times. Fifty-six mice died in traps (1.11 % of total captures). Out of 227 sub-adults captured, 65 (32 %) were caught in the winter of 2003 and 102 (50 %) were caught in the winter of 2004. Out of 67 reproductive females captured, 28 (42 %) were caught in the winter of 2003, 18 (27 %) were caught in the winter of 2004, and 15 (22 %) were caught in July 2004.

### Survival models

Seven of the original 30 models had a  $\Delta AIC_c \leq 7$  and were revised with individual covariates (Table 1). All of these structured survival periodically with regard to time. Virtually no support existed for structuring survival seasonally (0.009 summed weight for all seasonal models) or without a time effect (0.007 summed weight for all time invariant models).

Model *period* best explained the data, allowing survival to vary for each interval between primary periods but not spatially or by treatment (Table 1). The second best

model *period + neighborhood* added the 900 m spatial configuration and the third best model *period + thin=control* added a treatment effect with the thin treatment being equal to the control. Following guidelines suggested by Burnham and Anderson (2002), I characterize model *period + neighborhood* and model *period + thin=control* as having strong and moderate support, respectively, for consideration as the best approximating model, given uncertainty in the information criterion. Model *period* was only 2.70 times better than model *period + neighborhood* and 3.39 times better than model *period + thin=control*. Other models had little support.

Estimates of monthly adult survival rates from the top three models ranged from 0.57 (95 % CI = 0.47, 0.66; model *period + neighborhood*) to 0.80 (95 % CI = 0.75, 0.84; model *period + thin=control*). Sub-adult survival was 9 % less than that of adults (in model *period*  $\beta = -0.35$ , 95 % CI = -0.63, -0.07). Survival estimates for adults are given from model *period* in Figure 3, illustrating variation through time. There is a notable jump in survival in the fall after treatments were first applied, although this model does not include a treatment effect.

Confidence intervals for all treatment and spatial effects included zero, making survival estimates between models statistically indistinguishable. Still, treatment and spatial terms hold information, as evidenced by competitive model  $AIC_c$  values and a decrease in deviance (Table 1; Burnham and Anderson 2002). This information indicates trends in the data that can help evaluate hypotheses. Model *period + neighborhood* suggested group 1 had the highest survival rates, followed by group 3, group 2, unit 1, and finally unit 11. Units 1 and 11 were burn units. Model *period + thin=control*

suggests survival is lower on burn units and higher on thin/burn and herbicide/burn units, relative to the thin and control units.

Initial capture probabilities from model *period* ranged from 0.013 (95 % CI = 0.00, 0.10) to 0.53 (95 % CI = 0.37, 0.68). Behavior, age, and sex all affected capture probabilities. Effect sizes were the virtually the same for all models, since model parameterization was the same. Cotton mice responded positively to trapping, both within and between primary periods. Recapture rate was 35 % higher than the probability of initial capture (in model *period*  $\beta = 1.55$ , 95 % CI = 1.36, 1.73).

Individuals that had been captured during primary period  $i-1$  were 32 % more likely to be captured during primary period  $i$  (in model *period*  $\beta = 1.41$ , 95 % CI = 1.18, 1.63). Sub-adults were 5 % less likely to be captured (in model *period*  $\beta = -0.33$ , 95 % CI = -0.51, -0.15). Males were 2 % less likely to be captured (in model *period*  $\beta = -0.12$ , 95 % CI = -0.21, -0.02).

### **Recruitment models**

The top 11 models held 95.7 % of the  $AIC_c$  weight (Table 2). This can be viewed as a 95 % confidence set of models (Burnham and Anderson 2002). Any of the top four models could have been the one that best approximates truth, given the set of candidate models. These models had  $\Delta AIC_c < 3$ , held 76.8 % of the  $AIC_c$  weight, and had evidence ratios that compared favorably with the top model. All of these models contained effects for total area of source habitat within 900 m, average distance to source habitat within 900 m, and treatment. The parameterization that equates thin units to control units (*thin=control*) is a more parsimonious characterization of treatment effects than handling thin units separately (*trt*).

Seniority rates were high. Estimates from the top ranked model ranged from 0.55 (95 % CI = 0.42, 0.67) to 0.99 (95 % CI could not be calculated because the estimate was near the upper maximum likelihood boundary). Estimates of recruitment from model *period* show variation through time (Figure 4). Recruitment was highest in the summer and fall-spring period before treatment. After treatment, recruitment was highest in the fall, followed by the spring, and lowest in the summer.

Area of source habitat had a negative effect on seniority (in the top model  $\beta = -0.17$ , 95 % CI = -0.31, -0.03). Average distance to source habitat had a positive effect on seniority (in the top model  $\beta = 0.17$ , 95 % CI = 0.02, 0.32). The effect of burning on recruitment was 3 % to 4 % (in the top model  $\beta = -0.51$ , 95 % CI = -0.87, -0.16).

Other treatment effects could not be distinguished statistically from the controls. Regardless, the model selection process indicates the model terms for these treatments contain valuable information about recruitment. The top two models (with the *thin=control* parameterization) indicate that recruitment was highest on burn units, followed by herbicide/burn units, thin and control units, and finally thin/burn units. The third and fourth ranked models (with the *trt* parameterization) indicate the same order but with units with the thin treatment having higher recruitment than control units.

### **Population size and growth**

Population size estimates from model *period* ranged from 1.22 (95 % CI = 1.01, 5.65) to 63.30 (95 % CI = 13.97, 383.9). Populations generally showed a spike during the winter trapping season. Burn units had the highest observed rate of population growth for the three-year span of the study (Figure 5). Control units had the lowest rates,

showing declining populations. Thin/burn units showed stable or slightly declining rates. Thin units and herbicide/burn units showed mixed results.

## **DISCUSSION**

My goal was to conduct a thorough assessment of cotton mouse population dynamics through intense capture-recapture sampling under the robust design. This effort, in conjunction with a replicated, manipulative experiment, has yielded reasonably strong inferences regarding the effects of ecosystem restoration efforts on cotton mice. This is the first reported use of robust design modeling to estimate survival for adult and juvenile cotton mice, as well as seniority and recruitment estimates for cotton mice.

### **Treatment effects**

To interpret treatment effects, I discuss recruitment rates exclusive of the effects of source habitat. I refer to estimates of survival from the third ranked survival model, which included treatment effects.

My hypothesis that thinning would not alter the habitat in a way that affects cotton mice and that habitat quality on thin sites is similar to that of controls was supported. Survival and recruitment models that treated thin units equal to control units outperformed models that treated thin separately. Results do not support the hypothesis that cotton mice would be able to locate adequate resources to survive and reproduce on thin and control units. With the exception of one thin unit, control and thin unit population growth rates were much lower than 1.0, despite the general rise in survival rates. Thin and control units had the third lowest survival and recruitment rates, indicating habitat quality on these units was poor. Perhaps the shrub layer became so

dense that grasses and forbs were shaded out and the mice lost a valuable source of seeds, or the leaf litter became so deep that it was difficult for mice to forage for food.

I hypothesized that burning would improve habitat for cotton mice by increasing local availability of resources, with the thin/burn treatment causing the best improvement. This hypothesis was met with interestingly mixed results. The thin/burn treatment may have created sources. This treatment had the highest survival rates, the lowest recruitment rates, and population growth rates close to one. A source is expected to have a stationary population growth rate over several generations as resident individuals live long and only enough individuals are recruited to the population to replace those that die; excess individuals are exported (Pulliam 1988). One argument against this conclusion is that if the thin/burn treatment improved habitat, raising the carrying capacity, the size of the populations should have increased from pre-treatment levels. The population growth rate on two of these sites was 0.94, which could be viewed as too low to describe a source. The population growth rate on the third site was 1.04. These calculations were made from estimates of population size, which have an associated variance, so estimates of population growth rate are approximations. Real values could be higher or lower.

The herbicide/burn treatment also appears to have improved habitat for cotton mice. Two of these sites had growing populations. The herbicide/burn units had the second highest survival rates and recruitment rates, improved over control units.

Unlike the thin/burn treatment, the burn treatment appears to have created sinks. These units had the highest population growth rates and highest recruitment rates but the lowest survival rates. These rates are characteristic of a sink wherein turnover of individuals is high. Sinks can have population sizes much higher than that of sources

(Pulliam 1988) and a newly created sink could exhibit a rapidly growing population as animals displaced from sources spill into the area.

One possible explanation for the difference between the thin/burn and burn treatment is that the combination of thinning and burning had a synergistic effect. Opening the shrub layer by fire and the canopy by thinning allowed light to reach the forest floor so the beneficial effects of fire could be realized. On burn sites, where thinning was absent, it may be that not enough light reached the forest floor for the beneficial effects of fire to be realized, leaving only a burned-out understory that provided few resources for mice. This does not explain how the herbicide/burn treatment improved habitat. An alternative explanation is that the combination treatments did a better job of opening the shrub layer, allowing the herbaceous layer to flourish, whereas burning alone was not enough to sufficiently open the shrub layer to benefit the herbaceous layer.

Results indicate treatments had a stronger effect on recruitment than survival. The top ranked survival model included no variation in survival estimates. The *thin=control* parameterization of survival ranked third and estimated treatment effects included zero in the 95 % confidence interval. This implies variation in survival rates between treatments was relatively small. Conversely, there was enough variation in recruitment between treatments that treatment models performed strongly in the recruitment analysis and zero was not included in the estimate of the 95 % confidence interval for the effect of the burn treatment. Even small differences in survival between treatments could cause noticeable changes in the population growth rate, as evidenced by high seniority estimates (Nichols et al. 2000).

### **Source habitat effects**

Results provide circumstantial support for the hypothesis that bottomland hardwood forests and swamps serve as sources for cotton mice. Results supported my hypothesis that bottomland hardwoods close to experimental units would provide immigrants to those units. Recruitment increased with an increase in the total area of bottomland hardwoods within 900 m and decreased as the average distance to bottomland hardwoods within 900 m increased. Models that combined both source habitat and treatment effects ranked highest in the recruitment analysis. This is the first use of landscape variables in capture-recapture modeling to infer the immigration of animals from source habitat outside the study area.

This difference in immigration between experimental units caused by availability of source habitat did not obscure treatment effects on population size. By ranking units in descending order of population growth rate, a clear pattern of treatment effect emerges (Figure 5). The three burn sites had the highest rates, thin/burn sites had stable (or nearly stable) rates, and control sites had the lowest rates. This pattern is coincident with estimates of recruitment and survival from models including treatment terms. The pattern was not perfect as one herbicide/burn unit and one thin unit were not in the expected order. Neither this departure from expected order, nor the rankings of units within treatments were explained by availability of source habitat.

### **Spatial effects on survival**

The rank of units by population growth rate within the thin/burn, thin, and control treatments is best explained by the *period + neighborhood* survival model. The strong contribution to population growth rate by survival apparently overshadowed differences

in recruitment between units caused by immigration from source habitat. There is no apparent explanation for the order of units with the burn and herbicide/burn treatments. Again, estimates of population growth rate do not account for variation in population size estimates, so failure to achieve an exact match between observed population growth rates and model predictions is not surprising.

Model selection did not favor models that included the *unit* or *locale* spatial terms, indicating populations could not be defined over these smaller areas. Defining the cotton mouse population requires some resolution greater than the 570 m radius used for buffers to define the *locale* model. This resolution may be large, as the top ranked survival model contained no terms of spatial segregation.

### **Habitat quality, vital rates, and spatial scale**

Defining habitat quality requires delimiting the boundaries of the habitat and linking vital rates to the delimited area (Garshelis 2000). These two objectives are notoriously difficult to obtain. Habitat is usually defined arbitrarily from a human perspective and vital rates are rarely measured in studies of habitat quality. I constructed models that linked vital rates to habitat defined at various scales, based upon insights from cotton mouse biology. Model selection results show that vital rates operated over multiple scales. The top three survival models each defined habitat on a different scale. The top model (*period*) defined habitat as the entire study area. The second ranked model (*period + neighborhood*) defined habitat at an intermediate scale. The third ranked model (*period + thin=control*) defined habitat by treatments, which were applied to small, 15 ha stands. Recruitment also varied at different scales due to quality of habitat both outside and within experimental units. Some of these results are surprising. It is

easy to understand how the survival of a mouse that lives on a 0.5 ha home range is determined by local habitat quality. It is not as intuitive to think about survival rates for the population as being determined by habitat defined over a large area.

Defining the scale at which vital rates operate provides a better idea of the appropriate size area for restoration projects. In my study, treatments applied to 15 ha stands were probably not large enough to substantially effect the population; rather they caused localized departures in vital rates within the larger population. Information about the size of populations and the space they require to function is also very important for determining the necessary size of wildlife refuges. Community membership within a management or conservation area may be determined, in part, by the available pool of species living outside the area but within dispersal range.

### **Management implications**

Small mammals play a key role in ecosystem function (Grant and French 1980, Brown and Heske 1990, Talmon et al. 2003) and therefore judging the success of ecosystem restoration efforts should include consideration of the effects on the small mammal community. Assuming cotton mice represented the small mammal community, combining fire with thinning or herbicide appeared to have the greatest impact, and therefore may be the quickest method for restoring the ecosystem. Had treatments been carried out over a larger area, treatment effects might have been more substantial. Applying restoration efforts over a large area would mimic the fires that once burned over great distances in the longleaf pine ecosystem.

Results indicated that cotton mice populations in the upland were supported, at least in part, by immigration from sources outside the management area. Maintaining

refuges of source habitat can help mitigate the effects of forest management on the small mammal community. Managers should be cognizant of how their actions might attract immigrants from outside the management area.

Although a treatment effect was apparent in population growth rates, interpretation of these rates alone could lead to false conclusions. Without information about survival, the high estimates of recruitment and population growth on the burn units could give the impression that the treatment had a positive effect. Managing animal communities requires assessment of changes in population demographics as they respond to habitat alteration at a local scale, within the context of the surrounding landscape. An accurate assessment of the effects of restoration actions on an animal population requires measurement of survival and reproduction within the restoration area and animal movement to and from the restoration area.

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## **TABLES AND FIGURES**

Table 1. Summary of model selection results for survival of cotton mice in Covington and Escambia Counties, Alabama, 2001-2004. Models are ranked in ascending order by Akaike's Information Criterion, adjusted for small sample size ( $AIC_c$ ). Top models all estimated a unique survival rate for each of nine intervals between trapping periods (period). Neighborhood and locale represent two spatial aggregations of experimental units. The neighborhood configuration was constructed by placing 900 m buffers around experimental units, while the locale configuration was constructed with a maximum 570 m buffer. Treatments were modeled in 1 of 3 ways: 1) each treatment – thin, burn, thin/burn, herbicide/burn, and control – was estimated to have unique effect (trt), 2) thin units were estimated to have the same estimates of survival as control units; all other treatments had a unique effect (thin=control), 3) all units that were burned were constrained to have the same estimate of survival; thin units were constrained to have the same estimates of survival as control units (burn).

Model	AIC <sub>c</sub> <sup>1</sup>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	K <sup>2</sup>	Deviance	Evidence <sup>3</sup> Ratio	Cumulative <sup>4</sup> Weights
period	17496.15	0.00	0.56	150	17186.76		0.56
period + neighborhood	17498.14	1.99	0.21	154	17180.23	2.70	0.76
period + thin=control	17498.63	2.48	0.16	153	17182.86	3.46	0.92
period + trt	17500.85	4.70	0.05	154	17182.95	10.50	0.97
period + locale	17502.72	6.57	0.02	155	17182.69	26.75	1.00
period * burn	17505.62	9.47	0.00	157	17181.32	114.14	1.00
period + burn	17539.27	43.12	0.00	151	17227.75	2.31E+09	1.00

<sup>1</sup> Akaike's Information Criterion corrected for small sample size

<sup>2</sup> Number of parameters

<sup>3</sup> Likelihood of the top ranked model versus the competing model (e.g., the top model is 2.7 times more likely to be the model that best approximates truth than the second ranked model).

<sup>4</sup> Sum of the AIC<sub>c</sub> weights from the competing model and each higher ranked model.

Table 2. Model selection results for recruitment of cotton mice in Covington and Escambia Counties, Alabama, 2001-2004. Models are ranked in ascending order by Akaike's Information Criterion, adjusted for small sample size ( $AIC_c$ ). Treatments were modeled in 1 of 3 ways: 1) each treatment – thin, burn, thin/burn, herbicide/burn, and control – was estimated to have unique effect (trt), 2) thin units were estimated to have the same estimates of survival as control units; all other treatments had a unique effect (thin=control), 3) all units that were burned were constrained to have the same estimate of survival; thin units were constrained to have the same estimates of survival as control units (burn). Area = total area of bottomland hardwoods within 900 m of each experimental unit. Avg dist = average distance to all 30 m map cells containing bottomland hardwoods within 900 m of each experimental unit.

Model	AIC <sub>c</sub> <sup>1</sup>	Δ AIC <sub>c</sub>	AIC <sub>c</sub> Weight	K <sup>2</sup>	Deviance	Evidence <sup>3</sup> Ratio	Cumulative <sup>4</sup> Weights
area + avg dist + thin=control	17787.17	0.00	0.33	64	17657.50		0.33
area * avg dist + thin=control	17788.10	0.92	0.21	65	17656.37	1.59	0.54
area + avg dist + trt	17788.91	1.74	0.14	65	17657.18	2.38	0.68
area * avg dist + trt	17789.89	2.72	0.09	66	17656.11	3.90	0.77
avg dist + thin=control	17790.92	3.75	0.05	63	17663.30	6.52	0.82
area * avg dist	17791.77	4.59	0.03	60	17670.29	9.94	0.85
thin=control	17791.87	4.69	0.03	62	17666.29	10.46	0.88
area * avg dist	17792.25	5.08	0.03	62	17666.68	12.67	0.91
avg dist + trt	17792.86	5.68	0.02	64	17663.18	17.15	0.93
period * burn	17793.51	6.33	0.01	61	17669.98	23.73	0.94
trt	17793.61	6.44	0.01	63	17665.99	25.00	0.96

<sup>1</sup> Akaike's Information Criterion corrected for small sample size

<sup>2</sup> Number of parameters

<sup>3</sup> Likelihood of the top ranked model versus the competing model (e.g., the top model is 2.7 times more likely to be the model that best approximates truth than the second ranked model)

<sup>4</sup> Sum of the AIC<sub>c</sub> weights from the competing model and each higher ranked model.

Figure 1. Map of Auburn University's Solon Dixon Forestry Education Center, site of the Fire/Fire Surrogate Study's Gulf Coastal Plain location, showing experimental design, 900 m buffers for spatial segregation of units, and location of bottomland hardwoods and swamps.

Figure 2. Treatment and trapping schedule for a replicated experiment and capture-recapture study of the effects of fire and fire alternatives on small mammals in longleaf pine stands, Covington and Escambia Counties, Alabama, 2001-2004.

Figure 3. Monthly survival rates and 95% confidence intervals, estimated for each interval between primary trapping periods (model *period*), for cotton mice in Conecuh and Escambia Counties, Alabama, 2001 – 2004.

Figure 4. Monthly recruitment rates and 95% confidence intervals, estimated for each interval between primary trapping periods, for cotton mice in Conecuh and Escambia Counties, Alabama, 2001 – 2004. Recruitment in the summer of 2003 was almost zero. Confidence intervals for an estimate approaching the maximum likelihood boundary cannot be calculated accurately.

Figure 5. Population growth rates for a three-year span from 2001 to 2004, ranked in descending order, for populations of cotton mice living on experimental units treated for habitat restoration, in Covington and Escambia Counties, Alabama.

Figure 1.

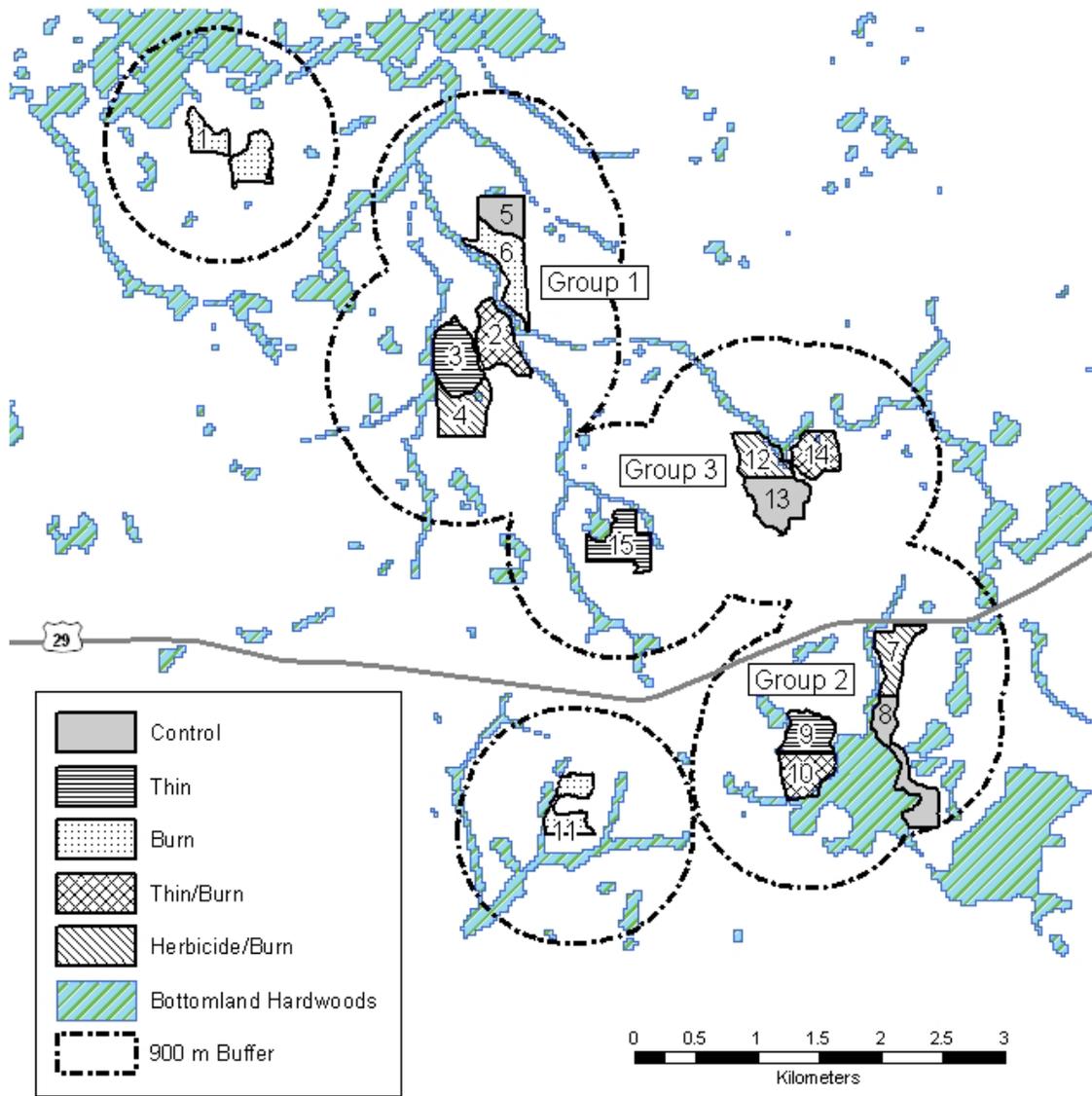


Figure 2.

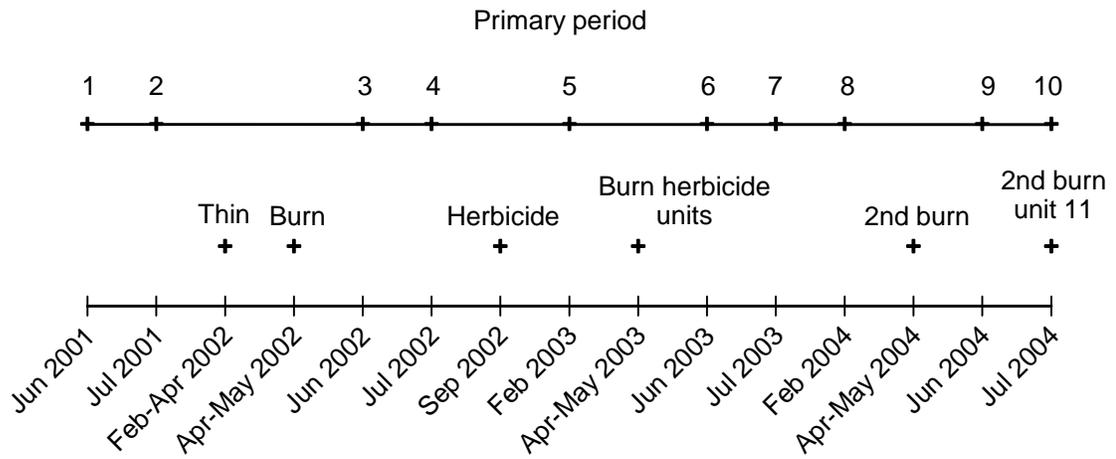


Figure 3.

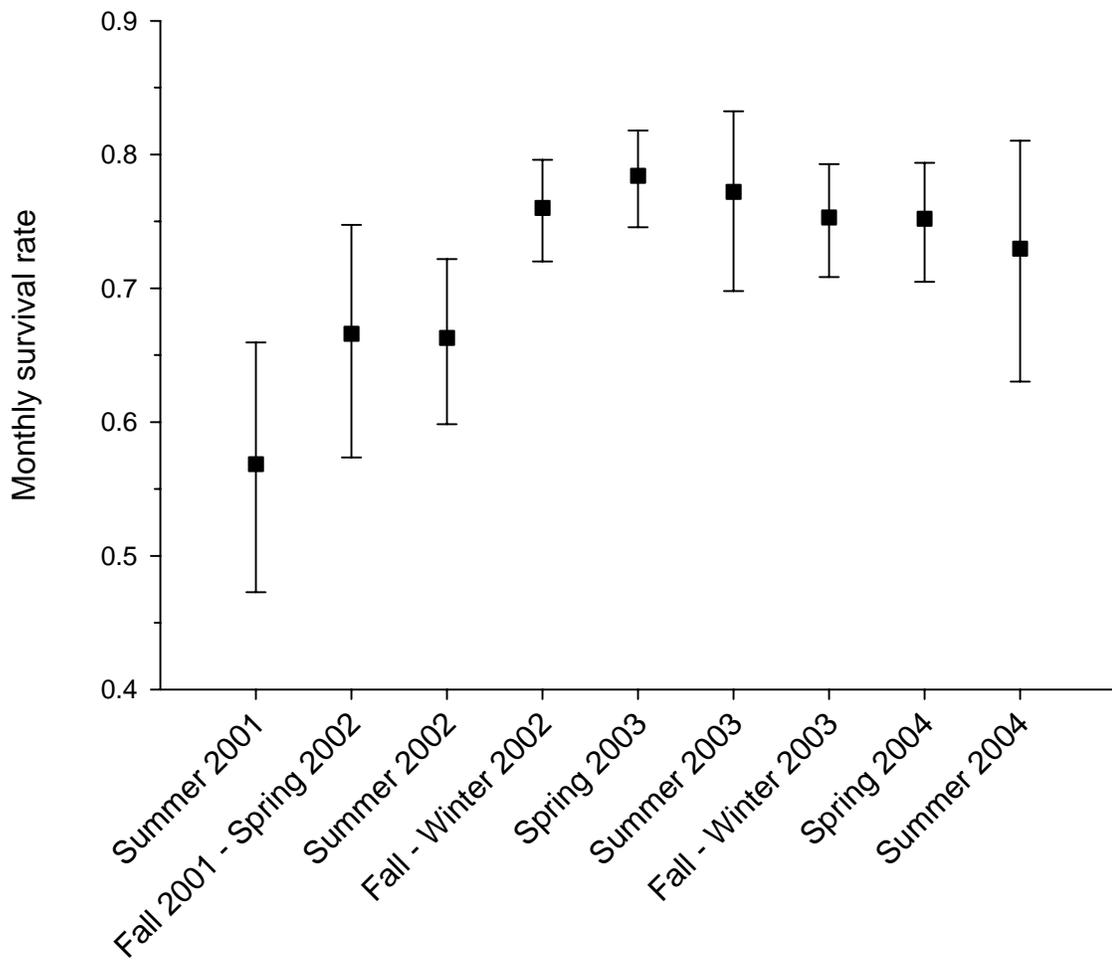


Figure 4.

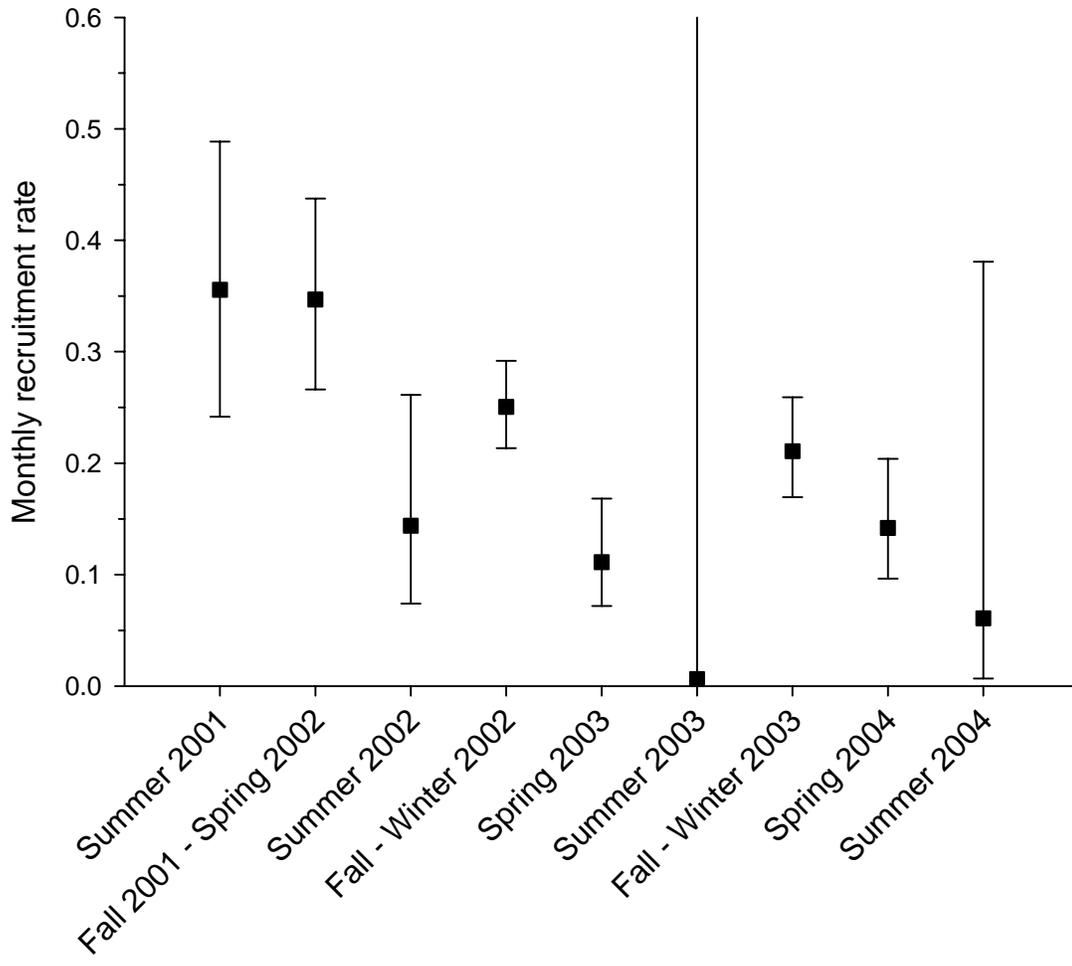
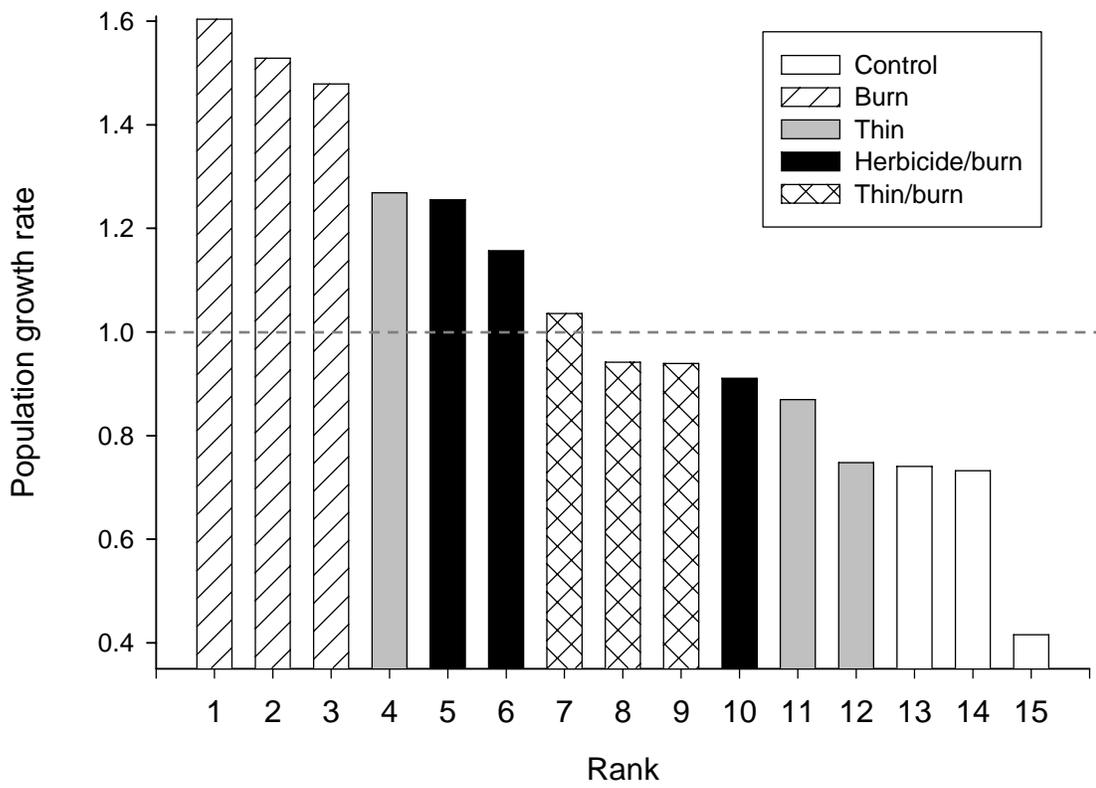


Figure 5.



RH: Small mammals of longleaf pine

RESTORING THE SMALL MAMMAL COMMUNITY OF A LONGLEAF PINE  
ECOSYSTEM

**Abstract:** Small mammals play a key role in ecosystem function and should be considered in any evaluation of the effectiveness of ecosystem restoration efforts. I participated in a replicated, manipulative experiment investigating the use of fire and fire alternatives to restore a longleaf pine ecosystem, formerly one of the most expansive and biologically diverse ecosystems of North America. I tracked changes in the small mammal community and species' demographics after application of restoration treatments. To define restoration goals for the small mammal community, I sampled a nearby longleaf pine savanna that was maintained by regular fires and resembled the historic condition. I found the reference small mammal community and the community to be restored differed in membership and structure. No changes in community structure were observed after treatment, but changes at the population level were evident; fire affected golden mouse (*Ochrotomys nuttalli*) survival negatively. Spring and summer survival rates for cotton mice (*Peromyscus gossypinus*) in the savanna were higher than those of cotton mice living in habitat being restored. Restoration of the small mammal community may be slow and several applications of fire may be required. Spring and summer survival rates for cotton mice in the savanna were also higher than those reported for the Key Largo cotton mouse (*P. g. allapaticola*) living in hammocks on Key Largo,

Florida, which contradicts the belief that hammocks provide optimal cotton mouse habitat. Optimal habitat for cotton mice may be a composite of longleaf pine uplands and hardwood bottomlands.

**Key words:** capture-recapture, demography, ecosystem restoration, fire, longleaf pine, *Ochrotomys nuttalli*, *Peromyscus gossypinus*, robust design, small mammals, survival

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Habitat restoration projects require measurable goals so that managers can determine whether restoration actions are having the desired effect and judge when restoration has been successful. Often restoration efforts are focused only on the floral community, but wildlife can play a key role in shaping the ecosystem (e.g., a guild of kangaroo mice (*Dipodomys* spp.) in the Chihuahuan Desert [Brown and Heske 1990], elephants (*Loxodonta africana*) in Africa [Dublin et al. 1990], and wolves (*Canis lupus*) in North America [Ripple and Beschta 2004]). A holistic approach to ecosystem restoration should define desired changes in both the floral and faunal communities.

Restoring fire-maintained ecosystems is now a concern in the United States. Decades of fire suppression policy have led to an annual epidemic of catastrophic forest fires across the nation. The Fire/Fire Surrogate (FFS) study, a collaborative effort between the United States Department of the Interior and the United States Department of Agriculture (Weatherspoon and McIver 2000) was designed to determine the most ecologically and economically efficient methods to reduce fuel loads and restore the nation's fire-maintained ecosystems. I measured the effects of experimental treatments on small mammals at the Gulf Coastal Plain site of the FFS study, where longleaf pine (*Pinus palustris*) savanna was the fire-maintained ecosystem to be restored.

Longleaf pine was once one of the most extensive forest types in North America (Landers and Boyer 1999), stretching from southeastern Virginia to eastern Texas (Frost 1993). The longleaf pine ecosystem supports a high diversity of plant species, making it one of the most species-rich communities outside of the tropics (Peet and Allard 1993). It is also home to the threatened gopher tortoise (*Gopherus polyphemus*) and indigo snake (*Drymarchon corais*) and the endangered red cockaded woodpecker (*Picoides borealis*). Today longleaf pine occupies < 3 % of its original range (Frost 1993). The loss of this expansive, unique, and species-rich ecosystem is of great ecological concern.

Early explorers to North America described expansive savannas featuring an open grass/forb understory and sparsely distributed longleaf pines forming open canopies (Platt 1999). These savannas evolved under a process of frequent fires ignited by the lightning strikes of spring storms (Platt 1999). Fires would burn at low intensity, sometimes over great distance, through the continuous grass understory (Frost 1993; Peet and Allard 1993). In the absence of fire, the fire tolerant species of longleaf pine savannas lose their competitive advantage over fire-intolerant species. Hardwoods eventually gain dominance in the canopy, shading out the pines, and a dense shrub understory develops, shading out the natural grasses, herbs, and longleaf pine saplings (Landers and Boyer 1999). Without fire, fuel loads build in the woody understory, which can lead to high intensity, crown-scorching wildfires (Peet and Allard 1993).

Information about the small mammal community of the longleaf pine ecosystem is sparse. No demographic information on small mammals living in longleaf pine stands exists. Boyer (1964) is the only researcher to document the small mammals of longleaf pine stands in Alabama. Out of 46 captures, he caught 25 oldfield mice (*Peromyscus*

*polionotus*), 14 cotton mice (*P. gossypinus*), 4 least shrews (*Cryptotis parva*), 2 eastern harvest mice (*Reithrodontomys humulis*), and 1 golden mouse (*Ochrotomys nuttalli*).

Few studies have examined how fire affects the small mammals of longleaf pine. Komarek (1939) reported changes in species present and their abundance in an experimental area in Grady County, Georgia, where fire was suppressed. Over 4 years, the understory changed from broomsedge and herbaceous ground cover to low bushes and tangles of vines. As the vegetation changed, the cotton rat (*Sigmodon hispidus*) population decreased while the cotton mouse and golden mouse population increased. Komarek called this change in the small mammal community a mammalian succession that was correlated with plant succession. He suggested that a mammalian climax community exists for each plant climax community.

Arata (1959) and Layne (1974) each conducted a study of burned areas near Gainesville, Florida. Arata (1959) studied an area covered with a dense understory of grasses and forbs dominated by turkey oak with few longleaf pine trees interspersed. This area had been burned in the last 3 or 4 years, which probably accounts for the open grass/forb understory. He found no change in the oldfield mouse or Florida mouse (*P. floridanus*) populations after fire, but cotton rats left the area. He felt that a low number of cotton rats in areas surrounding the burned site explained their failure to reoccupy the site once vegetation had returned to a density suitable for cotton rat habitation.

Layne (1974) studied a stand of slash pine (*Pinus elliottii*) and longleaf pine with a saw palmetto (*Serenoa repens*) and shrub understory before and after it was burned for the first time in 10 years. He showed a rapid increase in cotton mice after the fire. He also showed a fluctuation in the cotton rat population. Cotton rats left a burned area in

conjunction with the nearly complete loss of ground cover, but returned - in greater numbers than in the unburned area - after ground cover had grown back. The return of eastern harvest mice and cotton rats appeared to be related to the redevelopment of ground cover.

These studies were observational in nature and conclusions were based upon the numbers of individuals captured. Counting individuals does not account for variation in capture probabilities over time and space and therefore counts can be biased indices of population size (Williams et al. 2002). This may lead to inappropriate comparisons between sites. No study of fire in southern pinelands captured golden mice in numbers sufficient to suggest a response.

Many studies have examined the effects of habitat manipulation on small mammals, including the use of fire, herbicide, and mechanical removal of vegetation (e.g., Komarek 1939, Ahlgren 1966, Beck and Vogl 1972, Sullivan and Sullivan 1982, McMurry et al. 1996, Masters et al. 1998). While the specific results of these studies are as varied as the habitat types studied and the habitat affinities of the species living in them, the result common to most of these studies is that changes in the three-dimensional structure and content of the plant community cause changes in the structure and content of the small mammal community.

The FFS study at the Gulf Coastal Plain site was the first replicated, manipulative experiment to investigate the effects on small mammals of efforts to restore a longleaf pine ecosystem. The FFS study employed 4 treatments representing options for forest restoration: 1) control - no action was taken; 2) burn - prescribed fire was used to reduce fuel levels and maintain a frequent fire regime; 3) thin - trees were removed to reduce

tree density; 4) thin/burn - thinning was followed by prescribed fire. All treatments were replicated 3 times. These treatments were intended to result in a common desired future condition (DFC) - a forest stand structure and fuel level such that 80% of the trees would be able to survive a wildfire in all but the most unfavorable weather conditions.

The Gulf Coastal Plain site was located at Auburn University's Solon Dixon Forestry Education Center (Dixon Center) in south-central Alabama. The Dixon Center includes 2,130 ha of managed pine forestland. Sites selected for experimental units were longleaf pine stands in which the natural process of fire has been interrupted; hardwoods have grown into the canopy alongside the dominate longleaf pine and at the time of selection had a dense shrub understory dominated by yaupon (*Ilex vomitoria*). The Study Plan for the Gulf Coastal Plain site further defines the DFC as a stand structure like that of longleaf pine savannas: a canopy dominated by longleaf pine trees and an understory of grasses and forbs with some shrubs (Outcalt 2002). Herbicide is commonly used in pine plantations of the southeast to reduce understory vegetation that would compete with pine trees, and could help achieve the understory of grasses and forbs specified by the DFC. At the Gulf Coastal Plain site a 5th treatment was added to the 4 FFS treatments: herbicide/burn - herbicide was applied to the shrubby understory followed by prescribed fire.

To determine the DFC for the small mammal community, I expanded the study to include Compartment 58 of Conecuh National Forest (Conecuh NF), located near the Dixon Center. This site had a history of being burned during the spring every three years and resembled natural longleaf pine savannas; it was almost exclusively longleaf pine with a grass/forb understory. I used this site as a reference site or example of the small

mammal community found in local longleaf pine savannas. This allowed me to determine if the small mammal community living in the hardwood/pine woodlands at the Dixon Center differed from the community living in the pine savanna site of Conecuh NF, and track the progress of restoration towards the DFC.

To evaluate the difference in population demographics of species between treatments and between woodland and savanna, I conducted a capture-recapture study under Pollock's robust design (Pollock 1982, Kendall et al. 1995). I used the robust design in program MARK (White and Burnham 1999) to estimate abundance and survival rates for cotton mice and golden mice. The robust design provides the most precise estimates of capture probabilities available and thereby provides superior estimates of abundance and survival (Williams et al. 2002). I compared estimates for cotton mice in Conecuh NF to estimates for cotton mice at the Dixon Center to determine if there was a difference between the 2 locations. To determine whether restoration treatments affected survival of golden mice, I used program MARK to compare competing models of survival with and without treatment effects.

I expected the experimental treatments would cause changes in the plant community that would affect small mammals. Fire has several advantageous effects on vegetation. Soft mast and seed production increases after fire (Van Lear and Harlow 2000), grasses and forbs expand coverage of the forest floor (Brockway and Outcalt 2000), and resprouting vegetation is more nutritious and palatable (Stransky and Harlow 1981). Due to these beneficial aspects, I expected the habitat of Conecuh NF would be of higher quality for cotton mice than habitat at the Dixon Center. Golden mice prefer dense brush or thickets and are often found in association with greenbriar (*Smilax* spp.)

and honeysuckle (*Lonicera* spp.; Linzey and Packard 1977). I expected treatments would largely remove these habitat components, reducing habitat quality for golden mice. Cotton rats are closely associated with grassy habitats (Cameron and Spencer 1981), so I expected treatments to create favorable habitat for cotton rats.

I hypothesized longleaf pine stands maintained by frequent spring fires would support a structurally and compositionally different small mammal community than longleaf pine stands in which the natural process of fire has been interrupted. Since fire has beneficial effects on vegetation for cotton mice, savanna habitat should be of higher quality for cotton mice than woodlands. As treatments involving fire begin to shift the plant community from woodland to savanna, habitat quality for each small mammal species should change, altering each species' population demographics and causing a subsequent change in the community structure. Fire should degrade habitat quality for golden mice, but create favorable habitat for cotton rats. The structure of the small mammal community should shift from species preferring woodlands to species preferring savannas. Thinning alone should not substantially alter habitat quality for small mammals. Given my hypotheses, I predicted that: 1) captures in Conecuh NF would include small mammals with a preference for savanna habitat, 2) captures at the Dixon Center would include species with a preference for woodland habitat, 3) golden mouse survival and abundance would decline on burn, thin/burn, and herbicide/burn sites, 4) cotton mouse survival and abundance would be higher in Conecuh NF than at the Dixon Center, and 5) cotton rats would immigrate into units that were burned.

## MATERIALS AND METHODS

**Study area.**—The Dixon Center is located in Covington and Escambia counties in the Gulf Coastal Plain of south-central Alabama (31°9'N, 086°42'W). Summers in this region are hot and humid (often 35°C and 95% humidity), while winters are mild. Average annual precipitation is 14.22 cm (Outcalt 2002). Most precipitation occurs during late winter through spring and during afternoon showers in the summer. The terrain is relatively flat with rolling hills and ranges in elevation from 30 m to 100 m (Outcalt 2002).

Longleaf pine dominates much of the managed forest of the Dixon Center, but loblolly, slash, shortleaf (*P. echinata*), and spruce pine (*P. glabra*) are also abundant (Fischer and Holler 1990). Hardwoods can be found interspersed throughout the overstory and midstory in mixed pine-hardwood stands and concentrated along bottomland streams. Laurel oak (*Q. laurifolia*), white oak (*Q. alba*), and water oak (*Q. nigra*) are most numerous, while American beech (*Fagus grandifolia*), sweetgum (*Liquidambar styraciflua*), hickory (*Carya* spp.), maple (*Acer* spp.), ash (*Fraxinus* spp.), and elm (*Ulmus* spp.) also occur (Fischer and Holler 1990). The understory at the Dixon Center is dominated by yaupon, along with lesser amounts of blueberries (*Vaccinium* spp.) and gallberry (*I. glabra*; Outcalt 2002). In places yaupon forms shrubby thickets that are quite dense.

Compartment 58 of Conecuh NF lies approximately 14.5 km south of the Dixon Center (31.03° N, 086.64° W). This 155 ha stand was recently burned in the spring of 1996, 1999, and 2002. The overstory is exclusively longleaf pine. No midstory exists and the understory consists of grasses and forbs.

**Experimental design.**—The experiment at the Dixon center was laid out in a randomized block design. Three blocks were arranged by similar soil type and general location. Each treatment and the control were replicated 3 times, for a total of 15 experimental units. One replicate of each treatment and control was randomly assigned to an experimental unit in each block. Experimental units were 15.2 ha stands of mixed hardwoods and pine with a dense shrub understory. Minimum distance between experimental units was 156 m. I established 3 additional trapping grids in Compartment 58. The grids were in a line, the outside grids being 200 m and 280 m distant from the middle grid.

**Treatment and trapping schedule.**—All thinning took place between February and April 2002 (Fig. 1). Burn and thin/burn sites were burned for the first time in April and May 2002. Herbicide was applied in September 2002. Herbicide/burn sites were burned in the spring of 2003. A second burning of the burn and thin/burn sites was conducted in the spring of 2004. Due to weather conditions, one burn site was not burned a second time until July, after the first trapping period of the summer had taken place. Trapping followed Pollock's (1982) robust design. I conducted ten trapping sessions (primary periods), each comprising seven consecutive nights of trapping (secondary periods; Fig. 1). I trapped on each experimental unit twice during the summer for the 4-year duration of the study, with approximately one month between the two summer periods. I began winter trapping in February 2003 to gather more demographic data during the breeding season. I began trapping in Conecuh NF with the second primary period of the summer of 2002.

**Small mammal trapping.**—I sampled the small mammal community using standard capture-recapture methods. I installed a 0.81 ha trapping grid on each unit, locating most trapping grids in the center of each experimental unit. In some cases I opted to offset grids so as to avoid dirt roads. Each grid had 100 trapping stations, located at the intersection of 10 rows and 10 columns placed at 10 m intervals. I placed a single Sherman live trap, baited with sunflower seeds, at each trap station. I checked traps each morning. During the summer, I closed traps during the heat of the day and re-opened and baited them in the evening. During the winter, I placed batting in each trap for nesting material. Due to time constraints imposed by short winter days, I re-baited traps and left them open during the day.

I gave each newly captured animal a uniquely numbered ear tag (monel ear tags from Western Tag Co., Salt Lake City, Utah, USA). For every capture I recorded standard morphological measures and individual identification number. I released animals at the point of capture. This protocol was approved by Auburn University's Institutional Animal Care and Use Committee and complies with the guidelines of the American Society of Mammalogists (1998).

**Cotton mouse models.**—Using program MARK I ran the best model from the analysis of cotton mouse populations at the Dixon Center (Chapter 1). This model estimated a unique, monthly survival rate for each interval between primary trapping periods, but did not distinguish survival between treatments or experimental units. Since there were no treatments in Conecuh NF and I considered the 3 experimental units to be samples of the same population, I felt the top model from the Dixon Center analysis was appropriate for Conecuh NF. By using the same model for both locations, I was able to directly compare estimates.

**Golden mouse models.**—To evaluate the effects of time and treatment on golden mice survival at the Dixon Center I compared an a priori set of candidate models. These models are similar to those used for the analysis of cotton mouse survival (Chapter 1), but since the data set is much smaller, the underlying model structure is simpler.

A suitable goodness of fit test for the robust design is not currently available. The robust design in program MARK estimates apparent survival (survival and emigration), temporary emigration, initial capture probability, and recapture probability. I set program MARK to calculate monthly survival rates by defining the 9 intervals between primary periods in monthly units (e.g., 45 days = 1.5 month). I treated each experimental unit as a separate group. On 2 of the experimental units, only 1 golden mouse was ever captured. I did not include these 2 units in the modeling procedure, leaving 13 groups.

Data were too sparse to support complex models with numerous parameters. Since my interest was in survival, I used the same structure of temporary emigration, capture, and recapture probabilities for all models. I assumed that animals did not temporarily emigrate from the study area. This is a reasonable assumption because

golden mice are sedentary and have a home range  $< 0.6$  ha (Linzey and Packard 1977). I set the model to calculate one estimate of capture probability for each primary trapping period. I modeled a trap response within primary periods by setting recapture probabilities equal to initial capture probabilities plus an additive behavioral response. I modeled a trap response across primary periods by using the Huggins estimator (Huggins 1989, 1991) to include previous capture history as a covariate with capture probability. I defined previous capture history with a dummy variable indicating whether the individual had been caught in the previous primary period.

To determine whether survival varied temporally, I fit models with periodic and seasonal variation and a model with no temporal variability. The periodic model (*period*) estimated the same survival rate for the first 2 intervals between primary periods (due to sparse data) and estimated a unique survival rate for each period thereafter. The seasonal model (*season*) estimated a unique survival rate for each of 3 seasons defined by the time of year between primary periods – spring, summer, or fall-winter. Seasonal estimates did not vary between years.

I modeled treatments in three ways: 1) I handled each treatment as a separate effect on survival (*trt*). The 2 units that were removed from modeling were both thin/burn units. I treated the remaining thin/burn unit as a burn unit. 2) I constrained survival rates on thin units to be equal to those of control units, while the 2 other treatments were distinguished (*thin=control*), and 3) I constrained all units that were burned to have equal survival rates, while survival rates on thin units were equal to those of control units (*burn*). Because this later model only used 1 term for the treatment

effect, it was possible to model an interaction between time and treatment (*period\*burn*) without creating a model that contained more parameters than the data could support.

For all models, I constrained estimates of survival to be equal across all sites for the pre-treatment trapping periods. I added each of the 3 parameterizations of treatment effects to the *period*, *season* and null construction of time. To account for variation between units within treatments, I added a unit effect. I also included temporal models with no treatment effects, and a model with no variation in survival rates. All combinations of time, treatment, and unit effects constitute the candidate model set.

Model selection and inference followed the methodology of Burnham and Anderson (2002). I ranked models using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ; Akaike 1973). The model with the lowest  $AIC_c$  value is the most parsimonious approximation of truth among the set of candidate models, given the data. I used model deviance, the difference in  $AIC_c$  values between the top ranked model and each competing model ( $\Delta AIC_c$ ), and normalized  $AIC_c$  values (Akaike weights,  $w_i$ ) to compare the relative performance of competing models. Akaike weights can be viewed as the weight of evidence in favor of a particular model. The ratio of Akaike weights ( $w_i/w_j$ ), or evidence ratio, indicates the likelihood of one model over another (Burnham and Anderson 2002).

## **RESULTS**

**Community structure and membership.**—Ten species were caught at the Dixon Center and 7 species were caught in Conecuh NF (Table 1). Cotton mice were the most abundant species at both locations. Golden mice and southern flying squirrels (*Glaucomys volans*) were the second and third most frequently captured species in

woodland while cotton rats and eastern harvest mice were the second and third most frequently captured species in savanna. Four species caught at the Dixon Center were not caught in Compartment 58 – southern flying squirrel, eastern woodrat (*Neotoma floridana*), eastern chipmunk (*Tamias striatus*), and pine vole (*Microtus pinetorum*). Only one species caught in Compartment 58 was not caught at the Dixon Center – eastern harvest mouse (*Reithrodontomys humulis*). No oldfield mice (*P. polionotus*) were captured.

**Cotton mice.**—Estimated rates of survival for cotton mice in savanna habitat fluctuated much more widely than those for cotton mice living in woodland habitat (Fig. 2; Chapter 1). Fall survival rates were substantially lower in savanna habitat than in woodland habitat. Spring survival in the savanna exceeded that of woodlands. Summer survival was also higher in savanna than woodlands, but confidence intervals between the estimates overlapped. Estimates of abundance ranged from 0 (no individuals captured) to 55.05 (95% CI = 16.20, 228.58). Wide 95% confidence intervals made estimates of abundance indistinguishable from those of populations at the Dixon Center.

**Golden mice.**—Judging by  $\Delta AIC_c$ ,  $AIC_c$  weights, and evidence ratios, any of the top three models could have been the one that best approximates truth, given the set of candidate models (Table 2; Burnham and Anderson 2002). The top two models included the *burn* treatment structure – all units that were burned were constrained to have the same estimate of survival while thin units were constrained to have the same estimates of survival as control units. These two models hold 62.5% of the  $AIC_c$  weight. The third ranked model allowed no variation in survival estimates. While the fourth and fifth models had a  $\Delta AIC_c < 4$ , they had low weights and the evidence ratio indicated they did

not compare favorably with the top model. The fifth model had a deviance nearly identical to the null model but a larger  $AIC_c$  value, indicating the *thin=control* parameterization added no information.

The estimated effect of burning was a 13% reduction in monthly survival rates of golden mice (model *burn*  $\beta = -0.56$ , (95% CI = -1.11, 0.0004; model *season + burn*  $\beta = -0.53$ , 95% CI = -1.08, 0.01). The top ranked model, *burn*, estimated survival to be 0.72 (95% CI = 0.66, 0.77) on unburned units and 0.59 (95% CI = 0.47, 0.70) on burned units. Confidence intervals on estimates from model *season + burn*, the second ranked model, overlapped between burned and unburned units (Fig. 3). The estimated survival rate from the model containing no variation was 0.69 (95% CI = 0.63, 0.74).

The initial probability of catching a golden mouse was low (for model *burn* 0.04 to 0.16, 95% CI = 0.02, 0.11 and 0.08, 0.30, respectively). Golden mice responded positively to trapping, both within and between primary periods. Recapture rate was 35% higher than the probability of initial capture ( $\beta = 1.55$ , 95% CI = 1.36, 1.73). Individuals that had been captured at time  $i-1$  were 32% more likely to be captured at time  $i$  ( $\beta = 1.41$ , 95% CI = 1.18, 1.63).

Estimates of golden mouse abundance from the top model ranged from 0.00 to 43.10 (95% CI = 24.59, 97.31). Golden mice were captured before treatment on 6 of 9 units to be burned. They were eradicated from 2 sites after burning – a thin/burn unit and a herbicide/burn unit. The herbicide/burn unit held the largest estimated population of all golden mice. This occurred in the winter of 2003, after herbicide was applied but before the site was burned. Golden mice were only captured on 2 of 6 thin and control units prior to treatment. Through the course of the study, I caught golden mice on all of the

other thin and control units. Conversely, on 3 burned units I never caught golden mice, before or after treatment. Abundance estimates were too imprecise to distinguish between treatments or between pre-treatment and post-treatment periods.

**Cotton rats.**—Only one cotton rat was caught in more than one primary period. This individual was caught at the Dixon Center on a burn unit in March and June of 2004. This is the unit that was burned late in 2004. No cotton rat was caught in July 2004, after the second burning of the unit.

## **DISCUSSION**

**Community structure and membership.**—The woodland community differs from the savanna community in both structure and membership. The habitat generalist, the cotton mouse, dominates both. Other members of these communities are more specialized in habitat preference. Members of the woodland community require components found there – flying squirrels require nest cavities in deciduous trees, golden mice prefer thick tangles of vines and shrubs. The savanna community is filled with species that specialize in grassland habitat – the cotton rat and the eastern harvest mouse. Abundance appeared to be more evenly proportioned between species in the savanna, but this observation is based on the number of individuals captured for each species. Besides the cotton mouse and the golden mouse, too few individuals were captured to calculate abundances. The southern flying squirrel was probably under-represented because traps were placed on the ground. The trapping method was also inadequate to sample shrew populations.

**Cotton mice.**—Support was mixed for my hypothesis that frequently burned savanna is of higher quality for cotton mice than woodlands. Survival rates of cotton mice living in savanna were higher in the spring and summer, but lower in the fall, than rates for mice living in woodlands. The thin/burn and herbicide/burn treatments at the Dixon Center raised survival rates for cotton mice, indicating the beneficial effects of fire improved habitat (Chapter 1), which is consistent with higher spring and summer survival rates in the savanna. One possible explanation for low survival rates in savanna in the fall is the absence of hardwoods and a hard mast crop in the fall. At least 3 publications have noted a correlation between acorn production and an increase in the cotton mouse population (McCarley 1954, Pearson 1953, Stout 1976). Without a better understanding of low fall survival rates and mechanisms causing fluctuations in abundance, the relative quality of the savanna habitat is uncertain.

In the only other publication of survival rates for the cotton mouse of which I am aware, Sasso and Gaines (2002) used the Jolly-Seber method (Jolly 1965, Seber 1965) to estimate mean 28-day survival rates for Key Largo cotton mice (*P. g. allapaticola*) living in 4 age classes of hammock. They reported no temporal variation in survival rates. Hydric and mesic hammocks, bottomland hardwood forests, and swamps (bottomland hardwoods) are purported to be optimal habitat for cotton mice (Wolfe and Linzey 1977). This assertion has not been supported by any demographic data other than abundance. The 4 mean estimates reported by Sasso and Gaines ( $0.68 \pm 0.04$ ,  $0.71 \pm 0.05$ ,  $0.74 \pm 0.03$ ,  $0.78 \pm 0.05$ ; 2002) all fall below the spring and summer estimates of survival for adults in Compartment 58 of Conecuh NF. This contradicts the assumption that bottomland hardwoods are optimal habitat for cotton mice. In Chapter 1, I cite evidence

of emigration from bottomland hardwoods to upland experimental units as circumstantial support for the hypothesis that bottomland hardwoods are source habitat for cotton mice. This apparent conflict begs more thorough sampling in both bottomland hardwoods and longleaf pine savannas. I sampled only 1 forest compartment in Conecuh NF; Sasso and Gaines (2002) sampled 4 hammocks, all on Key Largo. Sasso and Gaines (2002) did not distinguish between adult and juvenile survival, which may have resulted in slightly lower estimates. I found juvenile survival rates to be approximately 9% less than adult survival rates (Chapter 1).

A large portion of the cotton mouse range (Wolf and Linzey 1977) is concurrent with the former range of longleaf pine (Frost 1993), suggesting a common evolutionary history. Habitat available to cotton mice in the pre-settlement landscape of North America would have been hardwoods in low-lying areas and longleaf pine in the upland (Platt 1999). Both bottomland hardwood forests and longleaf pine savannas are subject to periodic disturbance (floods and fire, respectively), which may have caused cotton mice to frequently move between upland and lowland. I hypothesize optimal habitat for cotton mice is a composite of bottomland hardwood forests and longleaf pine. I suggest that landscapes, not habitat “patches,” are the scale of importance to cotton mice and the appropriate perspective for restoration of the longleaf pine ecosystem.

**Golden mice.**—Model selection results support the hypothesis that fire reduces golden mouse survival. The 13% reduction in monthly survival rates equates to a 90% annual reduction. This reduction could have been due to mortality or individuals leaving the trapping area. It appears that golden mice colonized thin and control units but were prevented from colonizing burned units. This observation may only be a spurious effect

caused by the extremely low probability of catching a golden mouse for the first time. It is difficult to further assess the effects of fire on golden mice abundance because estimates were imprecise. The high ranking of the null model indicates that the data were too sparse to support complex models of the structure of survival.

**Cotton rats.**—The hypothesis that burning would create favorable habitat for cotton rats was not supported. Other than the 1 cotton rat that took up residence on a burned unit, cotton rats did not immigrate onto units that were burned. Grasses on this site did expand in coverage after initial treatment, but they were eliminated after the second burn (personal observation), which probably explains why the cotton rat was not captured during the final trapping period.

**Management implications.**—The goal of ecosystem restoration is to re-instate a particular community to a location where it was known or thought to have previously existed before anthropogenic disturbance. Implicit in this goal is the concept that ecosystems are unique by virtue of inherent biotic and abiotic processes and each member of the community plays some role in these processes.

Small mammals can play a significant role in shaping the ecosystem by consuming seeds and arthropods and by disturbing the soil (Boyer 1964, Grant and French 1980, Brown and Heske 1990, Ostfeld et al. 1997, Talmon et al. 2003). Ecosystem function can be affected by changes in density or composition of the small mammal community (Grant and French 1980). Brown and Heske (1990) showed that 3 species of kangaroo rats (*Dipodomys* spp.) acting as a keystone guild were essential to prevent desert shrubland from converting to grassland. Restoring the small mammal community can be pivotal to restoring ecosystem function.

The community at the Dixon Center will have to undergo substantial change before it resembles the community in Conecuh NF. No changes in community membership due to treatments were observed; golden mice were not eradicated and cotton rats did not immigrate. Lowered survival of golden mice indicates changes at the population level have begun. Returning regular, spring fires to longleaf pine stands should re-instate the process under which this ecosystem evolved and thereby a community that persists under this process. Since I was not able to distinguish a difference in golden mouse survival between the 3 treatments that included burning, I cannot recommend which treatment is best. Results from Chapter 1 indicate the combination treatments are most effective. It may require several episodes of burning before substantial changes in the community take place. If the process is continued, eventually species preferring woodland habitat may retreat to bottomland hardwoods. The result may be an upland community that comprises fewer species.

A picture of the reference community helps define restoration goals and evaluate the efficacy of restoration efforts. Negative trends in golden mouse survival can be viewed positively because a species that is not a member of the desired upland community will probably retreat to the bottomland hardwoods, where it can find the shrubs and vines it prefers. In the context of restoring longleaf pine uplands, the removal of some species is expected. If focus were held only on the uplands, the perceived loss of species could be interpreted negatively as a loss of biodiversity. If the correct perspective for restoration of the longleaf pine ecosystem is a landscape of upland longleaf pine interspersed with bottomland hardwoods, as I have suggested, then species richness is not lost. Rather, some species will relocate. Some ecosystems, such as longleaf pine or pine

pocosins (Mitchell et al. 1995), may be naturally poor in small mammal species.

Biodiversity is a poorly defined concept and a legal quagmire (Bosselman 2004).

Management decisions should be based upon an understanding of the ecosystem in which management actions will occur.

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**TABLES AND FIGURES**

Table 1.—Total individuals captured over the duration of trapping, in hardwood-pine woodland and pine savanna in Covington and Escambia Counties, Alabama, 2001-2004.

Species	# Individuals	% of Total
Hardwood-pine woodland		
<i>Peromyscus gossypinus</i>	1190	0.84
<i>Ochrotomys nuttalli</i>	148	0.11
<i>Glaucomys volans</i>	47	0.03
<i>Sigmodon hispidus</i>	14	0.01
<i>Neotoma floridana</i>	4	0.00
<i>Oryzomys palustris</i>	3	0.00
<i>Tamias Striatus</i>	3	0.00
<i>Microtus pinetorum</i>	*	
<i>Blarina carolinensis</i>	*	
<i>Cryptotis parva</i>	*	
Total	1409	
Pine Savanna		
<i>Peromyscus gossypinus</i>	139	0.68
<i>Sigmodon hispidus</i>	33	0.16
<i>Reithrodontomys humulis</i>	27	0.13
<i>Ochrotomys nuttalli</i>	5	0.02
<i>Oryzomys palustris</i>	1	0.00
<i>Blarina carolinensis</i>	*	
<i>Cryptotis parva</i>	*	
Total	205	

\* Species known to be present but uncounted.

Table 2.—Model selection results for golden mouse survival in longleaf pine stands undergoing treatments for habitat restoration in Covington and Escambia Counties, Alabama, 2001-2004. Models are ranked in ascending order by Akaike's Information Criterion, corrected for small sample size ( $AIC_c$ ). Effects of time were modeled seasonally or periodically. For seasonal structure (season) the intervals between primary periods were defined as spring, summer, or fall-winter and one estimate of survival was calculated for each of the three seasons. For periodic survival (period) a unique survival rate was estimated each of the 9 intervals between primary periods. Treatments were modeled in 1 of 3 ways: 1) each treatment – thin, burn, thin/burn, herbicide/burn, and control – was estimated to have unique effect (trt), 2) thin units were estimated to have the same estimates of survival as control units; all other treatments had a unique effect (thin=control), 3) all units that were burned were constrained to have the same estimate of survival; thin units were constrained to have the same estimates of survival as control units (burn). Individual effects for each experimental unit were included, representing variation between units within treatments.  $K$  = number of parameters. Evidence ratio indicates the likelihood of the top ranked model versus the competing model (e.g., the top ranked model is 2.31 times more likely to be the model that best approximates truth than the second ranked model).

Model	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	AIC <sub>c</sub> Weights	K	Deviance	Evidence ratio
burn	1938.81	0.00	0.44	14	1909.89	-
season + burn	1940.48	1.67	0.19	16	1907.28	2.31
null	1940.61	1.80	0.18	13	1913.81	2.46
season	1942.09	3.28	0.08	15	1911.04	5.17
thin=cont	1942.72	3.91	0.06	14	1913.80	7.07
season + thin=cont	1945.04	6.23	0.02	17	1909.69	
period + burn	1946.43	7.62	0.01	21	1902.37	
trt	1946.51	7.70	0.01	16	1913.31	
season + trt	1947.17	8.36	0.01	18	1909.66	
period	1948.23	9.42	0.00	20	1906.36	
period*burn	1950.64	11.84	0.00	25	1897.73	
period + thin=cont	1951.36	12.55	0.00	22	1905.11	
period + trt	1953.47	14.66	0.00	23	1905.00	
unit	1958.03	19.23	0.00	24	1907.35	
season + unit + burn	1958.34	19.53	0.00	27	1900.94	
season + unit + thin=cont	1959.80	21.00	0.00	27	1902.40	
season + unit	1960.41	21.60	0.00	26	1905.25	
season + unit + trt	1961.72	22.91	0.00	28	1902.06	
period + unit + burn	1963.16	24.35	0.00	32	1894.35	
period + unit	1966.55	27.74	0.00	31	1900.04	
period*burn + unit	1966.86	28.05	0.00	36	1888.74	
period + unit + thin=cont	1968.04	29.23	0.00	32	1899.23	
period + unit + trt	1970.35	31.54	0.00	33	1899.22	

Fig. 1.— Treatment and trapping schedule for a replicated experiment and capture-recapture study of the effects of fire and fire alternatives on small mammals in longleaf pine stands, Covington and Escambia Counties, Alabama, 2001-2004.

Fig. 2.— Monthly adult survival rates and 95% confidence intervals, estimated for each interval between ten primary periods, for cotton mice living in hardwood-pine woodlands and pine savannas in Covington and Escambia Counties, Alabama, 2001-2004.

Fig. 3.— Monthly survival rates and 95% confidence intervals, estimated for each of three seasons, for golden mice on burned and unburned experimental units in Covington and Escambia Counties, Alabama, 2001-2004.

Fig. 1.

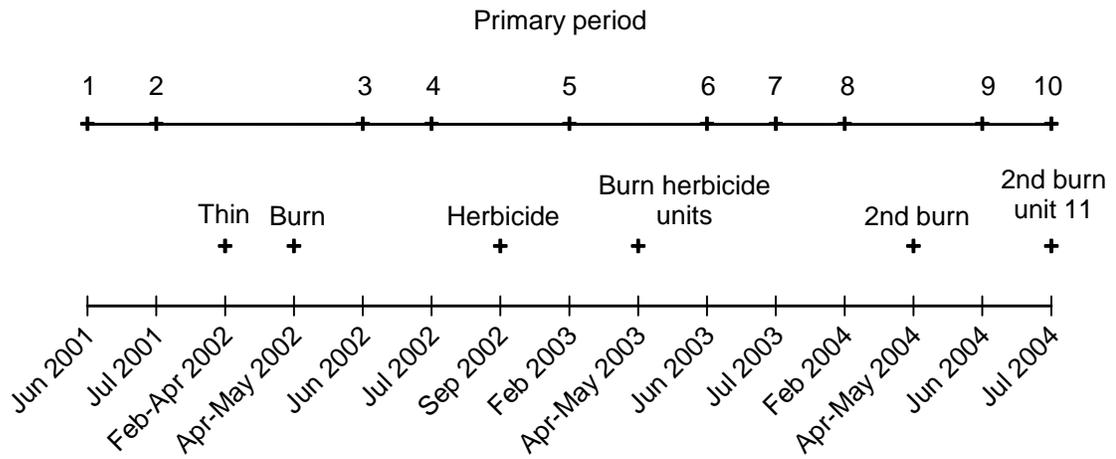


Fig. 2.

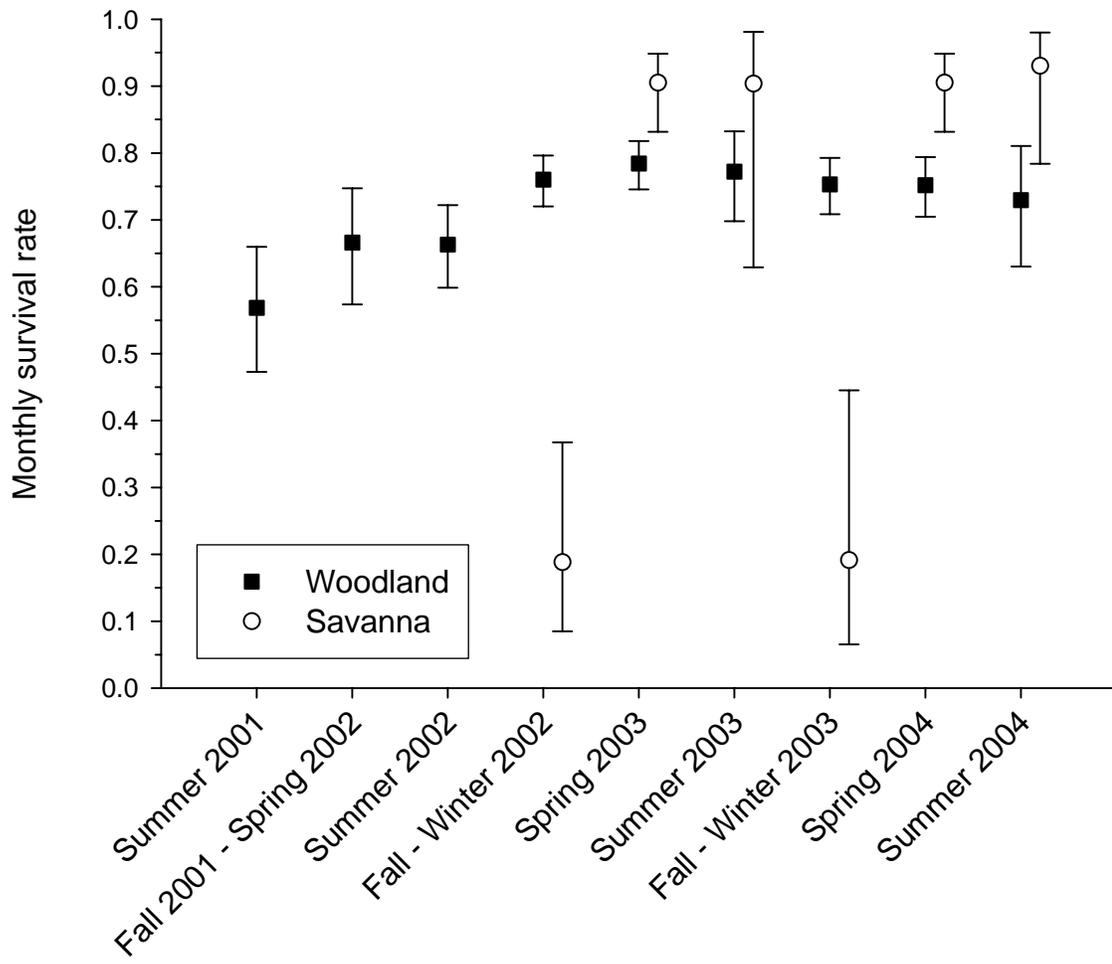
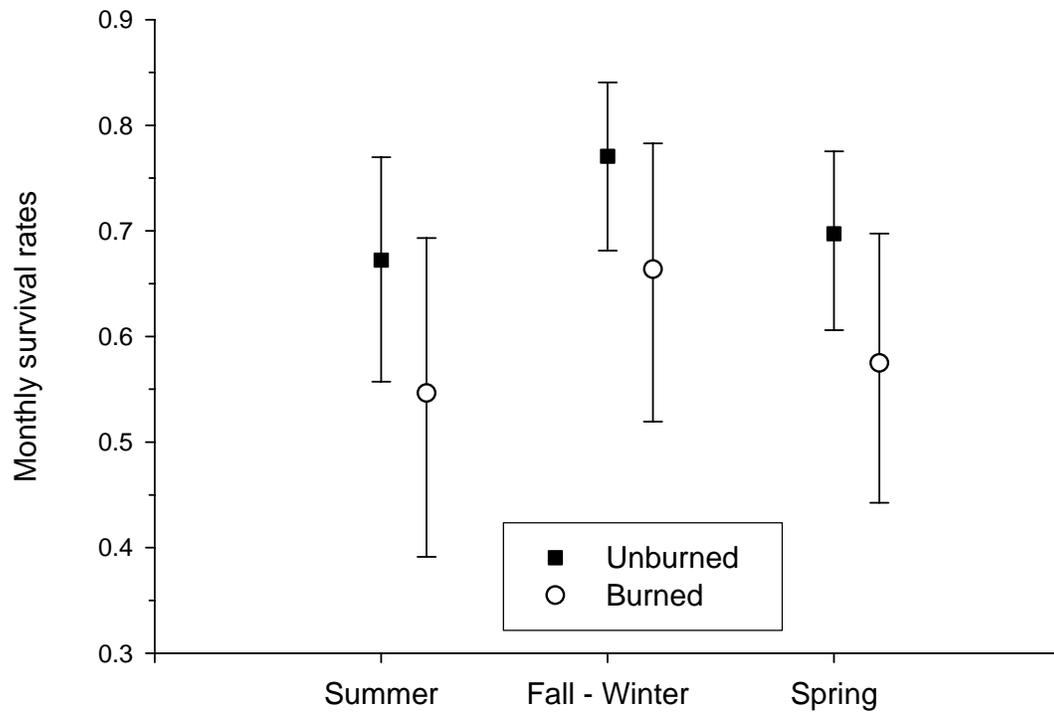


Fig. 3.



## CONCLUSION

The goal of my research was to investigate the effects of fire and fire surrogates (FFS) for ecosystem restoration on the small mammals living in longleaf pine stands in which the natural process of fire has been interrupted. To do so, I conducted a capture-recapture study to track changes in species' populations over time, space, and treatment. To make a full accounting of these changes, I hoped to quantify the four factors that determine population size – births, immigration, deaths, and emigration. I encompassed these four vital rates by calculating apparent survival (survival and emigration) and recruitment (births and immigration). I had hoped to distinguish births and immigration, but due to the lack of a distinct breeding season, the dispersal habits of juveniles, and too few data on reproductively active females, I was unable to do this. Despite this shortcoming, I feel I was able to construct a fairly detailed accounting of the effects of the FFS treatments on small mammals.

I conclude that the FFS treatments did affect small mammals, but only moderately. Treatments that combine fire with thinning or herbicide were most effective for ecosystem restoration. A treatment that included all three agents would probably be the most expeditious. Treatments should be applied over a larger area. In the early stages of restoration this may be difficult due to high fuel levels, but eventually fire should be carried out on a scale that mimics the fires that once burned over kilometers of longleaf pine savannas.

The small mammal community living in the hardwood-pine woodland stands at the Dixon Center differs in membership and structure from the community living in the longleaf pine savannas of Conecuh NF. Several rounds of restoration treatments may be required before changes in the community are recognized. The species found in the community are determined, in part, by the pool of species available for immigration from areas surrounding the restoration area.

The concept of defining habitat for a small mammal over multiple scales, some of which are quite broad, is not one that is often considered. Innumerable studies have investigated small mammal interactions with microhabitat. While these natural history studies are certainly important, my findings suggest that conservation of populations may require scientists to enlarge the window through which they view small mammals.

My research raised several questions that should be addressed with future research. While I learned much about cotton mouse population demographics, information is still lacking about reproductive success in different habitats. Pournelle (1952) conducted the only detailed study of cotton mouse ontogeny and reproduction. Information from various habitats on litter size, neonate survival, and age at maturity would greatly enhance our understanding of cotton mouse populations.

More demographic studies are needed of cotton mice in longleaf pine savannas and bottomland hardwood forests. I believe that the cotton mouse's evolution as a habitat generalist may be linked to its history living in two intertwined, frequently disturbed, and therefore constantly changed environments.

Finally, my research has raised questions about the correct way to perform a reverse time analysis using the robust design. Typically, reverse time analysis is

performed simply by reversing the capture history. This may not be appropriate for the robust design, which contains secondary sampling periods within the primary periods. I believe the secondary periods are asymmetrical regarding time, and the appropriate approach to reverse time modeling in the robust design is to reverse the primary periods, but retain the forward time order of the secondary periods. Reverse time modeling is a relatively new tool in capture-recapture modeling and further consideration of the theoretical underpinnings regarding robust design modeling is needed.