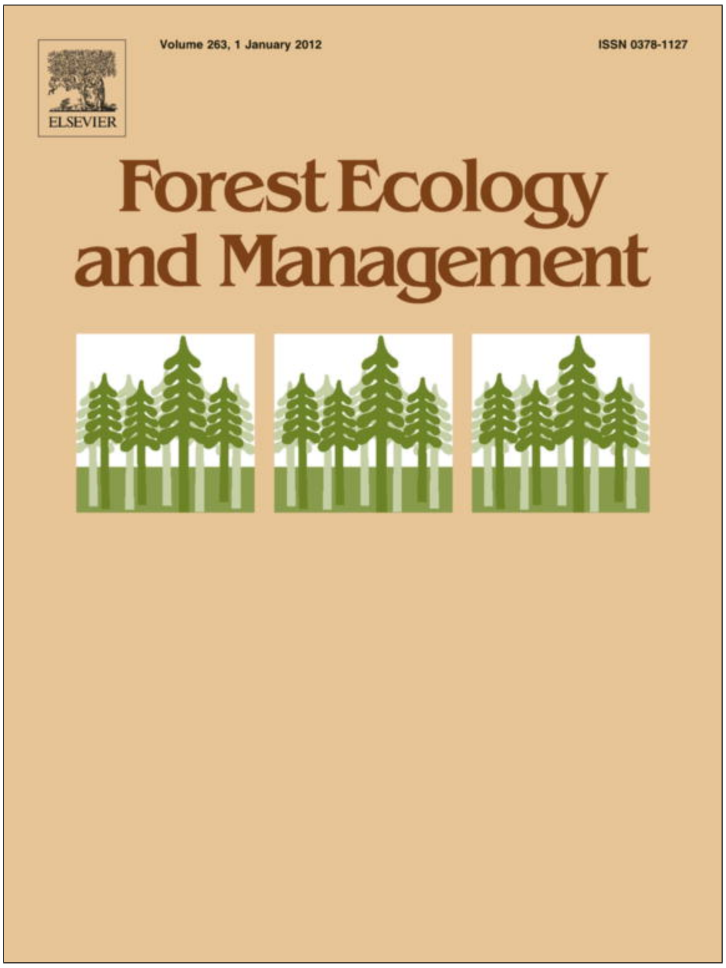
Volume 263, 1 January 2012
ISSN 0378-1127
ELSEVIER
Forest Ecology and Management

Forest Ecology and Management 271 (2012) 140–146

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Longleaf pine management practices and their impact on small mammal populations

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ARTICLE INFO

Article history:
Received 23 November 2011
Received in revised form 17 January 2012
Accepted 19 January 2012

Keywords:
Capture-mark-recapture (CMR) methods
Longleaf pine management
Herbicide application
Herbicide-fire combination
Prescribed fire
Survival rate

ABSTRACT

Rapid decline and degradation of longleaf pine ecosystems in the southeastern United States are conservation concerns. Prescribed fire is the primary management activity in this fire-dependent ecosystem, but prescribed fire is under increasing scrutiny, primarily due to air quality issues. There are concerns that prescribed fire may be removed, or replaced by herbicide, as a forest management tool without adequate understanding of the ecological consequences associated with such a change in management. We conducted a capture-mark-recapture study from April 1999 to April 2002 to examine experimentally the effect of prescribed fire, herbicide application and herbicide-prescribed fire combination on apparent survival rates of cotton mouse (*Peromyscus gossypinus*) and cotton rat (*Sigmodon hispidus*) populations. There was no evidence that herbicide application affected survival of cotton mice. Evidence to support effects of prescribed fire and herbicide-fire combination on survival of cotton mice was weak, although apparent monthly survival generally increased after these treatments. There was strong evidence that prescribed fire and herbicide-fire treatments affected survival of cotton rats, but the evidence for the effect of herbicide alone on survival was weak; survival rates declined in response to all three treatments but most strongly in response to the prescribed fire treatment. Fire alone had a stronger effect than an herbicide-fire treatment in both species. Without clear understanding of their ecological impacts, alternatives to prescribed fire should be employed with caution.

1. Introduction

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

Prescribed fire has been the primary management activity for the maintenance or restoration of this fire-dependent ecosystem (Frost, 1990; Glitzenstein et al., 1995; Streng et al., 1993). Every year, prescribed fire is applied to 1 million ha of forestlands in the southeastern United States to maintain native ground cover vegetation and to control encroachment of hardwood tree species (Cain et al., 1998; Richter et al., 1982). However, prescribed fire is under increased scrutiny due to perceived air quality issues, particularly the emission of atmospheric particles and their potential impacts on human health (Sandberg et al., 2002). A possible alternative to prescribed burning involves the application of herbicides, which is free of smoke management issues, or herbicide in combination with prescribed fire, which can potentially reduce smoke-related problems (Brennan et al., 1998). Herbicide application, followed by prescribed fire, has been suggested to be more effective in restoring the longleaf pine ecosystem than the use of prescribed fire alone (Brockway and Outcalt, 2000). The use of herbicide for modifying wildlife habitats and for invasive plant control

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doi:10.1016/j.foreco.2012.01.031

has increased in commercial pine plantation of southern United States (Miller and Miller, 2004). There are concerns that prescribed fire may be removed, or replaced by herbicide, as a forest management tool without adequate understanding of the ecological consequences of replacing (or augmenting) prescribed fire by herbicide.

Many wildlife species inhabiting longleaf pine ecosystems depend on habitat structure and resources that are maintained by frequent low intensity fires (Brennan et al., 1998). The population-level response of small mammals to prescribed fire is fairly well understood (Arata, 1959; Conner et al., 2011; Landers, 1987; Morris et al., 2011a,b), but we are not aware of studies that investigated the effect of herbicide, alone or in combination with prescribed fire, on small mammals inhabiting longleaf pine habitats. To fill this gap in knowledge, our goal was to provide data on the population-level impact of aforementioned longleaf pine ecosystem management practices on small mammals inhabiting the longleaf pine ecosystem. Specifically, we experimentally tested whether and to what extent survival rates of two of the most abundant and widely distributed rodent species found in the longleaf pine ecosystem (cotton rats (*Sigmodon hispidus*) and cotton mice (*Peromyscus gossypinus*)) were affected by herbicide, prescribed fire and the combination of the two. The population-level responses of these two rodents with different life history strategies will increase understanding of the ecological effects of these management practices.

2. Materials and methods

2.1. Study area

This study was conducted at the Joseph W. Jones Ecological Research Center in Baker County, Georgia. This 12,000 ha site is located on the upper coastal plain and is managed as research, education and conservation site. This is primarily a longleaf pine and wiregrass (*Arista stricta*) ecosystem with associated hardwood tree species, wetlands, slash pine and a variety of other habitats (Atkinson et al., 1996). Prescribed fire is the dominant management practice on the site, and individual burn units are burned on approximately 2-year intervals during the growing season.

2.2. Study species

Cotton mice are the most common and abundant semi-arboreal small mammals of pine forests in southeastern United States (Clark and Durden, 2002). Abundant woody materials and logs, and short overstory are an important microhabitat components for cotton mice (Mengak and Guynn, 2003). They utilize underground refuges such as gopher tortoise burrows, stump holes and root boles which provide them with cooler temperatures in summer as well as protection from fire and predators (Frank and Layne, 1992). Young are weaned in 2–3 weeks and the average life span is about 1.7 months (Wolfe and Linzey, 1977). Litter size ranges from 1 to 7, with an average of 3.7 (Pournelle, 1952).

Cotton rats are also abundant across the southeastern United States. These solitary, crepuscular rodents occur in many habitats, but require dense grasses, herbs and shrubs for food and cover (Goertz, 1964). Cotton rats start breeding as early as 2 months of age, and few survive >6 months (Odum, 1955). Cotton rats are an important prey species for a variety of predators and the primary cause of mortality is predation (Cameron and Spencer, 1981; Morris et al., 2011a). Cotton rats are characterized by high fecundity rates and their prolific breeding coupled with substantial predation mortality leads to population turnover in 5–8 months (Goertz, 1964).

2.3. Field Methods

This study was conducted at four different upland sites with sandy soils within the Jones Ecological Research Center from April 1999 to April 2002. Each site was divided into three plots, and each plot was randomly assigned one of three treatments: (1) prescribed fire alone, (2) herbicide application, followed by prescribed fire, and (3) herbicide application alone. Therefore, 12 treatment plots (three treatment × four replicates) were established. The size of each treatment plot was $\geqslant 8$ ha; most were considerably larger because the plots were delineated using existing roads and firebreaks.

Small mammal trap stations were placed along three systematically located transects within each plot. Transects were placed 100 m apart and 10 trap stations were placed on each transect with 15 m between stations, and at each station two Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida, USA) were placed approximately 1 m apart. During each trapping session, traps were set for 4 consecutive days. Traps were baited with rolled oats. Each captured small mammal was identified to species, weighed, sexed and released at the capture site. Cotton rats were marked individually with ear tags on both ears, and cotton mice were marked by toe clipping. Grids in each site were trapped every two months from April 1999 through November 2001, and after an interval of 5 months in April 2002 (the last trapping session).

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

2.4. Capture-mark-recapture (CMR) analysis

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

Monthly apparent survival (S), capture probability (p) and transition probability (ψ) from juvenile to adult state were estimated and modeled using multistate CMR models (Nichols et al., 1992; Williams et al., 2002). Cotton rats weighing >50 g (Bergstrom and Rose, 2004) and cotton mice weighing >19 g (Bigler and Jenkins, 1975) were classified as adults. Models were built for program MARK version 6.1 (White and Burnham, 1999) with R package RMark 2.13.0 (R Development Core Team, 2011; Laake and Rextad, 2008). Goodness of fit tests using the median $\hat{c}$ approach in program MARK provided no evidence for lack of fit for either species (cotton mice: $\hat{c} = 0.997$; cotton rat: $\hat{c} = 0.969$). Akaike's information criterion corrected for small sample size (AICc) was used for model comparison and statistical inferences (Burnham and Anderson, 2002; Williams et al., 2002). Using this approach, competing models with differences in AICc (ΔAICc) of <2 are considered equivalent; $2 \leqslant \Delta\text{AICc} \leqslant 4$ suggests evidence for differences among competing models, $4 \leqslant \Delta\text{AICc} \leqslant 7$ suggests substantial evidence for differences among competing models, and $\Delta\text{AICc} > 7$ is indicative of overwhelming evidence for differences in support of competing models (Burnham and Anderson, 2002).

Preliminary analyses were conducted to identify appropriate base models for S, p and ψ such that treatment effects could then be added in the subsequent analyses. For all analyses, probability of transition from adult to juvenile states was fixed to zero because such transitions are not biologically plausible. The base model for p

was investigated with time dependent S and ψ, taking into account the potential influence of trapping session, year, sex, season, site, state and their additive and two way interactive effects on p. The resulting best-supported model for p, along with time dependent ψ, was then used to investigate the base model for S, taking into account the influence of factors that could potentially affect survival; trapping session, year, sex, season, site, state, and additive and interactive effect of site and year. Finally, the base models for p and S were used to investigate the appropriate base model for ψ, taking into account the effect of trapping session, year, sex, season and site.

Changes in cover and food resources brought about by prescribed fire, herbicide application, and their combination, can last for several months; thus, effects of these treatments could influence cotton mice and cotton rat survival for varied amounts of time (Morris et al., 2011a). Therefore, we first investigated the best effect window for each of these treatments on survival of both species, using the base models identified in preceding analyses. For each treatment, we investigated three different effect windows (2, 4 and 6 months). We did not examine treatment effects beyond 6 months to avoid the potentially confounding effect of annual variation in survival rates.

Each of our study plots received one of the three treatments during the second year of the study; thus, during a given capture interval we placed each plot into one of three period categories: control (periods of time before treatments were applied or after treatment windows closed); treatment (plots and periods of time when a given treatment was in effect); and other (plots and periods of time when the other two treatments could have been in effect, set with a broad window: June 2000–December 2000 for fire and fire herbicide combination and February 2000–July 2000 for herbicide). We constrained survival rates to be the same for all control intervals except for the variation induced by the base model, and allowed survival to vary for 2, 4 and 6 months following treatment in that particular plot. The best-supported effect windows for each treatment were compared with base models that did not include the treatment effect in question, but which did include the 6-month treatment window for the other two treatments. Therefore, for each treatment we compared a model that divided survival into three categories (control, treatment, and other) with a model that divided survival into two categories (control [including treatment] and other). In this way we could test for the effects of each treatment separately while accounting for variation in survival induced by the other treatments.

3. Results

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

Overall monthly apparent survival was 0.78 ± SE 0.01. Monthly probability of transition from juvenile to adult state was 0.83 ± 0.05.

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

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

Model	K	AICc	ΔAICc	Model weight
Capture probability (p)				
p (Sex + time)	49	2857.685	0.000	1.000
p (Season[a])	36	2877.717	20.032	0.000
p (Season $*$ sex)	40	2884.881	27.196	0.000
p (Sex + year)	37	2892.513	34.827	0.000
p (.)	33	2899.125	41.440	0.000
Survival (S)				
S (site[b] $*$ year)	45	2832.129	0.000	0.853
S (year)	36	2836.227	4.098	0.110
S (site + year)	39	2838.412	6.283	0.037
S (season)	37	2864.851	32.722	0.000
S (site)	37	2867.724	35.595	0.000
Transition (ψ)				
ψ (Year)	32	2811.428	0.000	0.798
ψ (Site)	33	2814.782	3.354	0.149
ψ (.)	30	2818.078	6.650	0.029
ψ (Sex)	31	2819.790	8.362	0.012
ψ (Season)	33	2819.822	8.394	0.012

Note: Individuals weighing more than 19 g were classified as adults.
[a] Season: winter (December 21–March 19), spring (March 20–June 20), summer (June 21–September 22) and fall (September 23–December 20).
[b] Site: four different burn units within the Jones center.

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

Model	K	AICc	ΔAICc	Model weight
Fire effect window				
S (fire effect up to 2 months)	34	2810.666	0.000	0.499
S (fire effect up to 4 months)	34	2811.198	0.531	0.381
S (fire effect up to 6 months)	34	2813.513	2.847	0.120
Herbicide effect window				
S (herbicide effect up to 2 months)	34	2810.155	0.000	0.524
S (herbicide effect up to 6 months)	34	2811.732	1.577	0.238
S (herbicide effect up to 4 months)	34	2811.737	1.582	0.238
Combined effect window				
S(effect up to 6 months)	34	2810.914	0.000	0.623
S (effect up to 2 months)	34	2812.713	1.780	0.253
S (effect up to 4 months)	34	2814.163	3.250	0.123

There was evidence that fire (ΔAICc improvement of 1.877) and herbicide-fire treatments (ΔAICc improvement of 1.612) increased apparent monthly survival of cotton mice (Fig. 1) relative to the respective base models (Table 3). With regard to the herbicide only treatment, the base model was more parsimonious, suggesting herbicide had no effect on survival of cotton mice.

Cotton rats – From April 1999 to April 2002, we captured 969 individual cotton rats 2218 times. The sex ratio of captured individuals was approximately even. Initial analysis revealed that cotton rat capture probability varied seasonally; apparent monthly survival was time-specific; and transition probability from juvenile to adult was sex-specific (Table 4). Time-dependent survival models indicated that survival varied for each capture occasion; however, this model was not helpful for testing for treatment effects

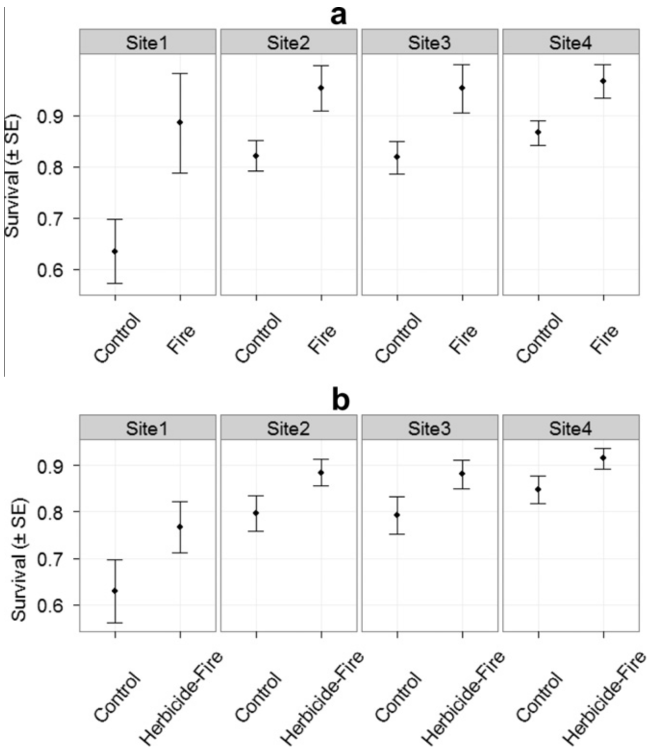

Fig. 1. Effect of prescribed fire (a) and herbicide – fire combination (b) on monthly apparent survival (±SE) of cotton mice at the Jones Ecological Research Center, Newton, Georgia in the year 2000. Sites are four areas within the center selected for the study.

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

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

because herbicide and fire treatments were applied in two different seasons, and season and treatment effects could have been confounded. Thus, we selected the top-ranked model that did not include season and short-term time effects (i.e., *S* (site + year)) as the base model for evaluating treatment effects (Table 4).

Overall apparent monthly survival was 0.67 ± 0.01. Probability of transition from juvenile to adult was 0.91 ± 0.04.

Analyses to investigate the best effect window for different treatments did not reveal strong support for any particular effect window (except for the fire effect window). We selected the top-ranked model for further analysis: a treatment effect on survival lasting up to 6 months after the treatment (Table 5).

There was strong evidence that prescribed fire (ΔAICc improvement of 17.80) and the herbicide - fire combination (ΔAICc improvement of 7.85) influenced survival of cotton rats (Table 6), but there was less evidence for the herbicide effect (ΔAICc improvement of 1.452). Interestingly, evidence for the effect of fire alone was stronger than the additive effect of herbicide and fire. Apparent monthly survival declined following all treatments (Fig. 2), and this decline was more pronounced after prescribed fire.

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

Model	*K*	AICc	ΔAICc	Model weight
Capture probability (p)				
p (Season)	36	1665.190	0.000	0.972
p (Constant)	33	1673.116	7.926	0.018
p (Sex)	34	1674.893	9.703	0.008
p (Site)	37	1678.178	12.988	0.001
Survival (S)				
S (time)	36	1665.190	0.000	1.000
S (season)	24	1701.667	36.477	0.000
S (site + year)	26	1717.285	52.095	0.000
S (year)	23	1719.939	54.749	0.000
S (site)	24	1721.549	56.360	0.000
Transition (ψ)				
ψ (Sex)	22	1638.486	0.000	0.654
ψ (Year + sex)	21	1640.942	2.456	0.192
ψ (Season + sex)	23	1641.950	3.464	0.116
ψ (Constant)	24	1645.314	6.829	0.022
ψ (Year)	24	1645.782	7.297	0.017

Note: 1. Only four models of capture probability were able to estimate all parameters of interest. 2. Individuals weighing more than 49 g were classified as adults.

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

Model	*K*	AICc	ΔAICc	Model weight
Fire effect window				
S (fire effect up to 6 months)	14	1673.031	0.000	0.971
S (fire effect up to 4 months)	14	1680.144	7.113	0.028
S (fire effect up to 2 months)	14	1686.941	13.910	0.001
Herbicide effect window				
S (herbicide effect up to 6 months)	14	1691.231	0.000	0.551
S (herbicide effect up to 2 months)	14	1693.031	1.800	0.224
S (herbicide effect up to 4 months)	14	1693.031	1.800	0.224
Combined effect window				
S (effect up to 6 months)	14	1676.264	0.000	0.551
S (effect up to 4 months)	14	1676.743	0.479	0.434
S (effect up to 2 months)	14	1683.476	7.211	0.015

4. Discussion

The statistical evidence for effects of prescribed fire and herbicide–fire on survival of cotton mice was not as strong observed for cotton rats. However, the increased survival of cotton mice associated with fire and fire-herbicide treatments is particularly interesting and suggestive that cotton rats and cotton mice respond to these treatments in very different ways. Local availability of soft masts and seeds, important food resources for cotton mice,

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

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

generally increases post-fire with beneficial effects on omnivorous rodents such as cotton mice (Sharp et al., 2009). A greater versatility in refuge selection and preference for underground sites such as stump holes and gopher tortoise burrows as refuge (Frank and Layne, 1992) makes cotton mice less susceptible to direct detrimental effects of fire. This also makes them less vulnerable to increased risk of predation due to reduced vegetative cover (Derrick et al., 2010). Furthermore, the increase in survival following fire alone was higher than that observed after herbicide or herbicide-fire combination treatments, suggesting that application of herbicide, with or without fire, does not generally replicate the ecological effects of fire.

In contrast, all treatments substantially reduced monthly survival of cotton rats. This was expected because cotton rats are highly susceptible to predation by meso-predators (Conner et al., 2011), and require heavy vegetation cover to avoid predation. Other studies have also shown that survival rates of cotton rats in longleaf pine ecosystems declined after prescribed fire, primarily due to increased predation (Conner et al., 2011; Morris et al., 2011a), but we found no studies evaluating the effect of herbicide and the herbicide – fire combination on cotton rat survival within longleaf pine forest. Rehmeier et al. (2005) hypothesized that, in the long run, fire application could be beneficial due to increase in local availability of food and clearing of litter which may hinder cotton rat movements. This suggests that, for cotton rats, changes in habitat brought about by fire events would be detrimental due to increased predation risk in the short run but, in the long run, increased abundance in local food availability and maintennace of preferred habitat may be beneficial. All three treatments affected survival in the same direction; their strength differed, with prescribed fire having the strongest effect and

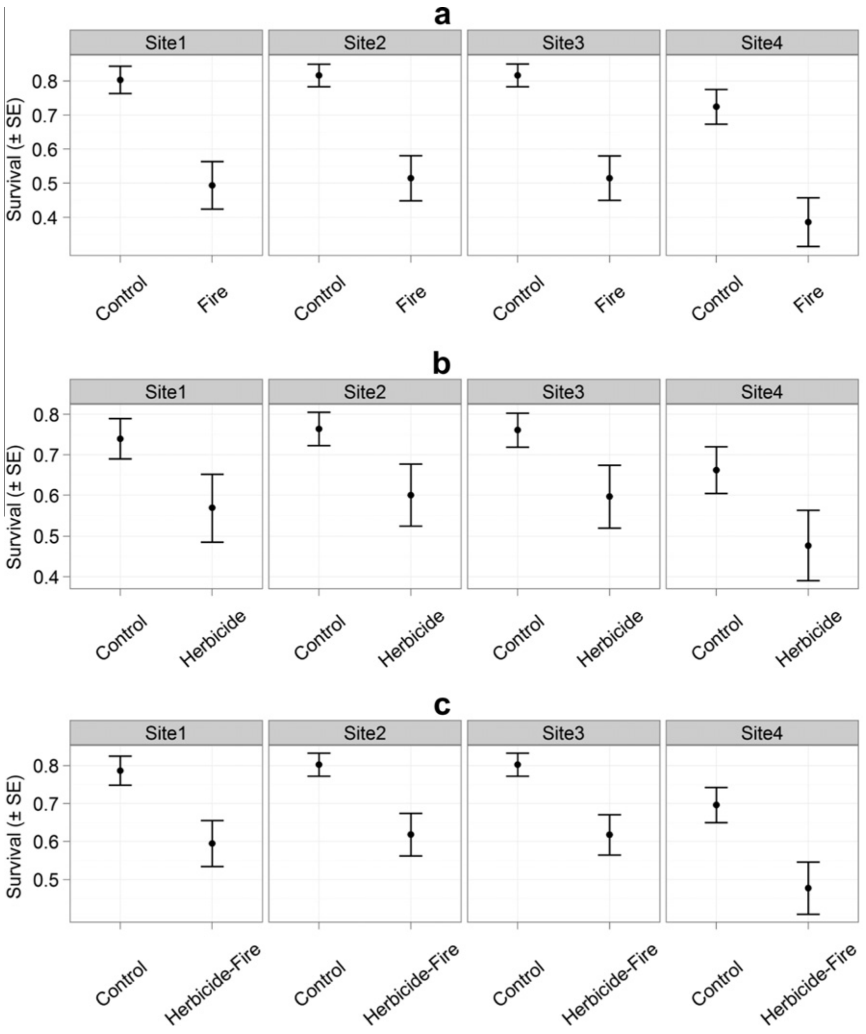

Fig. 2. Effect of prescribed fire (a), herbicide application (b) and herbicide – fire combination (c) on monthly apparent survival estimates (±SE) of cotton rat at Jones Ecological Research Center, Newton, Georgia in the year 2000. Sites are four areas within the center selected for the study.

herbicide application the weakest. The reasons for these differences are unclear. We hypothesize that different effects on vegetation cover brought about by these treatments had varied levels of influence upon the survival rate of cotton rats. Herbicide kills vegetation, but dead vegetation can still provide cover until it decomposes. On the other hand, fire results in immediate loss of cover. Furthermore, our herbicide application was directed towards hardwood and did not appreciably alter herbaceous cover available for cotton rats.

Management activities to restore structure, function and diversity of longleaf pine come with the potential risk for some species of special interest (Van Lear et al., 2005). Two species of small mammals with different natural histories responded differently to different longleaf pine management practices. Prescribed fire had opposite effects in these two species although for both species the strength of the fire effect declined with prior herbicide application. There was some evidence that herbicide application affected survival of cotton rats but there was no evidence that it affected survival of cotton mice. Although herbicide alone may mimic some of the ecological effects of fire, it apparently does not reproduce the same ecological effect of fire on cotton rat and cotton mice. The primary role of fire is to oxidize vegetation but it also provides a variety of other ecosystem services, such as releasing nutrients, seed scarification for germination and fertilization from ash and carbon. Reduction in understory litter after fire results in more sunlight on the ground which provides a favorable environment for many grasses and forbs to thrive. Herbicide also eliminates vegetation but it lacks many other ecosystem services provided by fire (Brennan et al., 1998). We are intrigued by the stronger effect of fire alone than herbicide-fire combination, but do not know the exact mechanism underlying this response. A possible explanation is that ecological effects of fire may be masked to some extent by a prior herbicide application. A complete understanding of ecological changes brought about by fire and the fire executed after herbicide application would require a detailed study of vegetative responses to these treatments.

Restoration of longleaf pine ecosystems requires restoration of the structure and function of the ecosystem as well as of ecological processes. Various management practices for the restoration of longleaf pine forests bring about different changes in ecological processes such that they have varied influences on the population dynamics of species inhabiting them. Long term studies are needed to elucidate the effects of management practices on other species of mammals, birds and reptiles to better understand the broader ecological impacts. Without clear understanding of these broader ecological impacts, alternatives to prescribed fire should be employed with caution because evidence suggests that ecological effects of fire are not reproduced by herbicide application, alone or in combination with fire. An ideal approach would be to use an adaptive management approach such that management decisions and our knowledge of ecological responses of longleaf pine ecosystems to alternative management strategies are integrated within one framework (Williams et al., 2002).

Acknowledgements

We thank all the field technicians who were involved in the fieldwork during the period of this study. Our warmest thanks are extended to M. Simmons who worked hard for the management of our database. Fieldwork was funded by Jones Ecological Research Center, and the graduate program for Binab Karmacharya was supported by the Department of Wildlife Ecology and Conservation, University of Florida and United States Foreign Fulbright Program Division.

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