

EFFECTS OF MAMMALIAN PREDATOR EXCLUSION, SUPPLEMENTAL FEEDING,
AND PRESCRIBED FIRE ON SMALL MAMMAL POPULATIONS IN A LONGLEAF
PINE ECOSYSTEM

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2010

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“[T]hinking about rats, as low-down as it seems, can easily lead to thoughts about larger topics, such as life and death and the nature of man.”

- Robert Sullivan, *Rats: Observations on the History & Habitat of the City's Most Unwanted Inhabitants*

ACKNOWLEDGMENTS

I received much support during the course of this project. The University of Florida and the Joseph W. Jones Ecological Research Center provided funding, equipment, and manpower. My co-chairs Madan Oli and Mike Conner and committee member Mel Sunquist gave a great deal of assistance, especially with experimental design, analysis, and editorial suggestions for this thesis. I am also grateful for the help of numerous technicians who assisted with data collection, entry, and management. Cat Eddins and Jen Eells got the project off to a good start and helped work out early difficulties. Bonnie Fairbanks, Amanda Goldberg, and Jamie Utz held down the fort, catching and chasing many rats while I was away from the field for a semester. James Miller, Megan Munroe, and Jud Swart, braved the summer heat and gnats in pursuit of ridiculous number of rats. Evan Hill, Amy Kryzton-Presson, and Erica Rigsby braved heat, gnats, mosquitoes, and the absence of the lab's fearless leader in pursuit of even more rats and made tracking around the fire a success. Hayden Martin and Cliff Rushton brought the field work to a close and assisted with proofing tens of thousands of trapping records. Jimmy Atkinson, Scott Smith, Cat Eddins, and Briant Williamson carried out the prescribed burns. The Herpetology lab, especially Jen Linehan and Kelly McKean, caught many rat-eating snakes and cared for them until the snakes passed the radio collars. Anna Derrick showed me the smammaling ropes with such great enthusiasm my own almost seems normal. I am grateful for her advice which I am sure saved me from many mistakes and frustration. Brent Howze was helpful with many random aspects of fieldwork, especially with those relating to radio telemetry. Jean Brock, Michael Simmons, and John Merritt provided assistance with GIS, data management, and IT support respectively. Liz Cox acquired even the most obscure references with

great speed. I am also grateful for the support of the administrative staff at both the Jones Center and the Department of Wildlife Ecology and Conservation at UF.

Two individuals deserve special thanks. Jessica Rutledge provided assistance with field work, data management, equipment, and pretty much everything else imaginable. Jeff Hostetler provided much patient assistance with data analysis and also made editorial suggestions. I don't care to think about how much more difficult this would have been without the help of these two individuals.

I also thank my family and friends for their support and for not saying things like "Ew, rats!" all the times I talk about rats. I thank my personal aggravation of rat, and her less long-lived partner, for being highly entertaining despite a prickly nature, and for showing me many things about the ratty nature.

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Master of Science

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By

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August 2010

Chair: Madan K. Oli

Major: Wildlife Ecology and Conservation

Food resources and predation play important roles in determining small mammal population dynamics. Each of these factors may affect population parameters such as abundance, survival, and reproduction. These factors may also interact as individuals under predation pressure make trade-offs between exposure to predators and access to food resources. Fires consume food sources and reduce cover, which increases exposure to predators. For species that occur in areas with frequent fires, it is beneficial to consider how all of these factors affect populations of interest. This study used a capture-mark-recapture framework to experimentally examine how supplemental feeding, mammalian predator exclusion, and prescribed fire affected survival, abundance, and reproduction of cotton rats (*Sigmodon hispidus*), cotton mice (*Peromyscus gossypinus*), and oldfield mice (*P. polionotus*). Radio telemetry was used to assess home range size and overlap of cotton rats. Among cotton rats, prescribed fire events had the greatest effect, causing large drops in survival, abundance, and reproduction. Food supplementation increased survival, rates of transitions to reproductive states, and abundances but was not sufficient to prevent post-fire declines

in any of these parameters. This indicates that predation and emigration are responsible for fire-related declines in survival and abundance. Population-level effects of predator exclusion effects were small in magnitude. Predator exclusion was, however, associated with increased male home range size, indicating a response to perceived predation risk. Among cotton mice, survival was affected (increased) only by an interaction between burning and predator exclusion. Rates of transitions to reproductive states decreased in burn years but increased with the combination of feeding and predator exclusion. Feeding increased abundances. Among oldfield mice, survival and abundance were greater in predator exclusion areas than controls. Feeding and the interaction of feeding and predator exclusion also increased abundances. Rates of transitions to reproductive states declined during peak breeding seasons during which burning occurred such that breeding transitions in these seasons were lower than in non-peak seasons. Some of these effects can only be understood by assuming individuals make behavioral responses to predation risk to limit mortality.

CHAPTER 1 INTRODUCTION

Predation and access to food resources can have large and direct effects on small mammal populations. Field studies have shown food addition to be associated with increases in abundance and survival, changes in rates of immigration and emigration, earlier reproduction, and greater numbers of young produced per reproductive event (Taitt and Krebs 1983, Boutin 1990, Campbell and Slade 1995, Krebs et al. 1995, Hubbs and Boonstra 1997, Perrin and Johnson 1999). Experimental removal or exclusion of predators has been associated with increased densities (Schnell 1968, Weigert 1972, Meserve et al. 1993, Yunger 2004), increased survival (Meserve et al. 1993, Oli and Dobson 2003), earlier breeding (Arthur et al. 2004), and increased immigration (Taitt and Krebs 1983, Perrin and Johnson 1999).

Indirect effects related to these factors may also be common and often result from behavioral responses associated with changes in predation or food resources. For example, food addition may cause changes in intraspecific aggression, and decreases in home range sizes (Boutin 1990, Desy et al. 1990, Hubbs and Boonstra 1998). Increased levels of predation risk have been associated with decreases in home range size and alterations in habitat use (Desy et al. 1990, Dickman 1992, Arthur et al. 2004, Yunger 2004). Behavioral changes may in turn affect vital rates at the population level. For example, reductions in space use associated with predation risk may limit access to reproductive opportunities. Indirect effects may be as large as or larger than direct effects, and may either take the form and direction of direct effects, or cause unexpected effects (Pressier et al. 2005).

Although food and predation may individually have large impacts on a population, there is also a great deal of theoretical and empirical support for interactions between these factors (Taitt and Krebs 1983, Abrams 1983, 1984, 1991, 1992a, 1992b, 1993, McNamara and Houston 1987, Desy and Batzli 1989, Hubbs and Boonstra 1997, Clark and Mangel 2000). In a large-scale experiment examining the effect of food supplementation and predator exclusion on snowshoe hare (*Lepus americanus*) populations, Krebs et al. (1995) reported that food addition tripled population densities, predator exclusion doubled population densities, and the combination of treatments resulted in an eleven-fold increase in population densities. Similarly, Hubbs and Boonstra (1997) found that while feeding and predator exclusion treatments each individually increased survival of arctic ground squirrels (*Spermophilus parryii*), survival in a combined treatment plot was significantly greater than either treatment alone. Similar trends were found with respect to increased growth rates (Hubbs and Boonstra 1997) and decreasing home range size (Hubbs and Boonstra 1998), indicating a significant interactive effect on several aspects of species ecology and behavior.

These interactions may stem from the fact that foraging behaviors are likely to put individuals at greater risk of predation. An individual must make trade-offs between the need to acquire food and the need to stay safe from predators. Optimally, an individual should maximize fitness by minimizing risk of death by predation while maximizing food intake. Rates of food intake are important to avoid starvation and because reproduction is often associated with the quantity and quality of food available. A large body of theoretical research suggests that such trade-offs are common (reviewed in Lima and Dill 1989), may be complex, and may cause counterintuitive

effects (Abrams 1991, 1992a, 1992b, 1993). This is especially likely to be true in systems with complex food chains and competitive interactions between multiple predator and prey species. Effects of trade-offs may also depend on a species' life history and may change with breeding/non-breeding seasons (Abrams 1991).

Theoretical investigations are crucial to understand and predict predator-prey interactions; however, empirical field data are also necessary to test predictions made in theoretical studies. Unfortunately, relatively few studies have adequately examined these factors. Many studies that attempt to do so are aquatic in nature, focus on small temporal and spatial scales, and/or lack replication. Long term, replicated experimental studies that consider large spatial scales and examine predator-prey interactions between terrestrial vertebrates are rare because of the difficulties and expense required to adequately carry out such experimental studies (but see Krebs et al. 1995).

The primary objective of this study was to experimentally examine how predation and food resources affect small mammal survival, reproduction, and abundances in a longleaf pine ecosystem. This study was carried out over four and half years and over a large spatial scale. We focused on three target species common to the longleaf pine ecosystem: cotton rats (*Sigmodon hispidus*), cotton mice (*Peromyscus gossypinus*), and oldfield mice (*P. polonius*). Capture-mark-recapture methodologies were used to estimate population parameters. Space use, in the form of home range size and overlap, was additionally considered for adult cotton rats.

The roles of food resources and predation may take on new aspects for small mammal species following fires, which occur frequently (historically over intervals of one to five years) in longleaf pine ecosystems. Fires consume both herbaceous food

resources and vegetative cover which increases predation risk. Different small mammal species exhibit different short-term reactions to fires. Cotton rat populations decline dramatically (Layne 1974, Bock and Bock 1978) while cotton mice exhibit either a neutral or short-term positive response to fire (Shadowen 1963, Hatchell 1964, Layne 1974, Suazo et al. 2009). Oldfield mice do not appear to respond strongly to fire over the short term (Arata 1959, Odum et al. 1973, Suazo et al. 2009). All three of these species benefit from frequent fire application over the long term (Masters et al. 2002, 2007, Suazo et al. 2009). While the long term benefits of fire are likely related to the maintenance of ideal habitat structure (Masters et al. 2002), the driving factors behind population changes over the short term remain poorly understood, although explanations relating to changes in food resources or cover, and by extension predation risk, are generally hypothesized. Therefore, a secondary objective of this study was to experimentally examine the roles of predation and food resources in small mammal population changes following prescribed fires.

CHAPTER 2
EFFECTS OF PRESCRIBED FIRE, SUPPLEMENTAL FEEDING, AND MAMMALIAN
PREDATOR EXCLUSION ON COTTON RAT SPACE USE AND POPULATION
DYNAMICS IN A LONGLEAF PINE ECOSYSTEM

Introduction

Food availability and predation can have dramatic effects on small mammal populations. Abundant food resources have been associated with increases in reproduction (earlier and/or longer reproductive seasons, more young produced per reproductive event), survival, abundance, and immigration (Boutin 1990, Campbell and Slade 1995, Webb et al. 2005).

Predation may also have large effects. At its most basic level, predation removes individuals from a population causing an immediate decrease in abundance. Predation may also have sub-lethal effects relating to perceived risk of predation. These include changes in behavior such as reduced activity, changes in habitat use, decreased home range size, and delay in age of first reproduction or in the onset of a reproductive season (Lima and Dill 1989). Non-lethal effects that may result from these behaviors include decreased growth rates, poorer body condition, and decreased overall reproductive output (Hik 1995, Peckarsky et al. 2008). Non-lethal effects on prey demographics may be as important as or more important than direct consumption (Werner and Peacor 2003, Preisser et al. 2005).

Clearly, changes in population parameters caused by changes in food resources and/or predation can have significant effects on population growth and abundance. For rodent species which mature and reproduce rapidly ("fast" species), changes in reproductive rates can have especially large impacts at the population level (Oli and Dobson 2003).

Effects relating to predation and food resources do not occur in isolation. In the presence of predation pressure, individuals must make choices that balance predation risk with the need to engage in activities that put them at risk of predation such as searching for food (McNamara and Houston 1987, Abrams 1991). Individuals avoid foraging in areas where they are vulnerable to predators even if good forage occurs there, unless they are food stressed such that the risk of death by starvation outweighs the risk of predation. Similar tradeoffs may occur with respect to other behaviors, such as seeking out reproductive opportunities (Lima and Dill 1989, Clark and Mangel 2000).

For species such as the cotton rat (*Sigmodon hispidus*), the occurrence of fires causes a crisis of both food and predation. Fire consumes herbaceous vegetation that cotton rats require for cover from predators and which they also use as a primary food source (Whitaker and Hamilton 1998). Multiple authors have noted precipitous declines in cotton rat populations following fires (Arata 1959, Bock and Bock 1978, Rehmeier et al. 2005). We know of no studies that have attempted to experimentally determine the driving forces behind these declines, although hypotheses relating to food resources and/or predation are generally proposed.

Many studies have examined how predation affects individuals sub-lethally by influencing behavioral decisions; fewer have been able to connect these decisions to population-level effects. Fewer still have examined such effects on large spatial and temporal scales. Experimental manipulation of predators and food resources allows a better understanding of how predation and food resources influence both individual behaviors and population dynamics. We examined the effects of predation and food resource availability on demography and space use of cotton rats over the course of

four and a half years and through three prescribed fire cycles by experimentally manipulating presence of mammalian predators and food resources. Using capture-mark-recapture (CMR) and radio telemetry data, we determined the impact of food resources and predation on cotton rat space use and population dynamics in general and following prescribed fire events.

Methods

Study Site and Species

This research was conducted at the Joseph W. Jones Ecological Research Center at Ichauway in Baker County, Georgia. Ichauway is a 12,000 ha property consisting primarily of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) ecosystem. Longleaf pine ecosystems are characterized by a low-density longleaf pine over-story, a diverse, herbaceous groundcover, and an open, park-like mid-story (Van Lear et al. 2005). Hardwood tree species occur at limited levels. Frequent, low intensity fires are key ecological processes. Consequently, application of prescribed fire is a primary management tool throughout Ichauway; most sites are burned on a two year rotation (Atkinson et al. 1996).

Cotton rats are solitary, crepuscular rodents found abundantly across the southeastern United States. They occur in many habitats, but require thick cover, particularly in the form of dense grasses and shrubs (Goertz 1964). Cover is essential for protection from a wide range of avian, mammalian, and snake predators. Herbaceous material is also consumed as a primary food source and used in nest construction. Predation is the most common cause of death among cotton rats (Weigert 1972, Derrick 2007), and predation pressure is so strong that cotton rat populations experience near complete turnover in as little as five to eight months (Goertz 1964).

Experimental Design

In 2002, the Jones Center constructed four mammalian predator exclosures, each paired with a nearby control with similar habitat. Plots range in size from 35.94 to 49.09 ha. Exclosures are surrounded by 1.2 m tall woven wire fences which carry electrified lines along the top, middle, and bottom to discourage mammals from climbing over or digging under (the weave is large enough to allow small mammals and snakes to pass through). Although mammalian predators occasionally enter exclosures, regular monitoring by track counts and thermal camera surveys indicate significantly fewer mammalian predators in exclosures than controls (Conner et al. 2010).

In June of 2007, two exclosure and two control grids were randomly selected to receive a supplemental feeding treatment consisting of placing 113 g (4 oz) of rabbit chow in cans at every other station trapping grids in each control and exclosure (see below). Food was replaced every other week. Empty cans were placed on non-feeding grids. This treatment continued through August 2009. Images from trail cameras demonstrated that cotton rats, cotton mice (*Peromyscus gossypinus*), oldfield mice (*P. polionotus*), house mice (*Mus musculus*), woodrats (*Neotoma floridana*), flying squirrels (*Glaucomys volans*), and eastern cottontails (*Sylvilagus floridanus*) regularly used feeding stations. We found no evidence that cans were defended by individuals of any species.

In February of 2005, 2007, and 2009, all plots were burned according to Ichaaway's burn plan which has these study areas on a two year burn rotation.

Field Methods

Each control and exclosure contains a 12x12 small mammal trapping grid with 15 m spacing between stations. Pairs of grids were trapped four times per year (once

each season) from January 2005 through June 2007 and eight times per year (twice per season) from July 2007 through the June 2009 using Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida, USA). A small amount of a granular insecticide was sprinkled around each trap to prevent deaths due to fire ants. New captures were marked individually with metal ear tags. Data recorded for all captures included location, species, sex, weight, age (adult or juvenile, based on weight), reproductive condition (for males, testes descended or not, for females, if pregnant and/or lactating or not), and hind foot measurement.

In four of the eight study plots (one fed predator exclosure, one unfed predator exclosure, one fed predator control, and one unfed predator control plot) cotton rats weighing 90 g or more (so that collar weight was not > 5% of the rats' mass) were anesthetized with Isoflurane and fitted with radio collars (Advanced Telemetry Systems Isanti, Minnesota, USA; Sirtrack Wildlife Tracking Solutions, Havelock North, New Zealand; and Telenax, Playa del Carmen, Mexico). Following recovery, rats were released at their capture site. Collared rats were located by triangulation or homing a minimum of three times per week and located visually once a week to confirm status as alive or dead. Rats were located using TRXC-2000S (Wildlife Materials Murpheysboro, Illinois, USA), R-1000 (Communication Specialists, Inc. Orange, California, USA), or R-2000 receivers (Advanced Telemetry Systems Isanti, Minnesota, USA). When rats were found dead, the location was searched for sign to classify the event as a slip or death due to avian, mammalian, snake, or unknown predation, handling, or unknown causes. If rats slipped or chewed off collars or if signals were lost, attempts were made to retrap and recollar rats. Searches for missing signals were undertaken if rats could

not be retrapped. Collaring and tracking began in July 2007 and continued through August 2009.

Collared rats were tracked intensively around the 2009 burn. Rats were homed on to verify status as alive one to two days prior to burning. Signals were monitored during the burn and rats were homed on again immediately after the fire. For seven days following the fire, rats were tracked twice a day. Rats surviving past seven days were tracked daily for an additional seven days. Regular monitoring was restored thereafter. Missing rats were searched for immediately to detect emigration.

Trapping, handling, and tracking methods followed recommendations of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Florida Institutional Animal Care and Use Committee.

Statistical Methods

Analysis of capture-mark-recapture (CMR) data

Capture-mark-recapture (CMR) data considered for this analysis included 26 sessions from January 2005 through June 2009. Analyses were carried out using the R 2.9.1 (R Development Core Team) package RMark 1.9.6 (Laake and Rexstad 2008) to build models for program MARK 6.0 (White and Burnham 1999). Capture probabilities were fixed to 1 for radio collared rats.

Multistate models were used to estimate and model state specific survival (S), capture probability (p), and transitions between reproductive states (Ψ). States used for S and Ψ were based on reproductive condition. Males were considered to be in reproductive condition if testes were descended, females if pregnant and/or lactating. Therefore, models evaluating effects on S which include a reproductive condition term estimate and model survival separately for reproductive and non-reproductive

individuals, and models evaluating effects on Ψ which include a reproductive condition term estimate and model probabilities of individuals moving between reproductive states (i.e., rates of non-reproductive individuals entering reproductive states, rates of reproductive individuals remaining reproductive).

Preliminary investigation considered the potential influence of trapping session, season, year, and the additive effect of season and year on p . Influence of reproductive condition and sex was assessed for S and Ψ . Breeding season was also considered for Ψ . Assessment of effects on p , S and Ψ was carried out in a sequential fashion. First, effects on p were considered while modeling S and Ψ using the most general models described above for each. Effects on S and Ψ were then considered in a similar fashion.

Assessment of goodness-of-fit was carried out using the median \hat{c} approach in program MARK (White and Burnham 1999). The median \hat{c} test indicated a mild overdispersion ($\hat{c} = 1.262$). Models in each parameter's set were compared using Akaike's information criterion corrected for small sample size (AICc), after quasi-likelihood adjustments (QAICc) made using $\hat{c} = 1.262$. Models were considered well supported if they had a Δ QAICc of less than two. The best supported model within each parameter's set was selected a base for modeling that parameter in further analyses.

These analyses indicated that reproductive condition and sex modeled in an interactive fashion ($S(\text{reproductive condition} * \text{sex})$), were important for describing S (Table 2-2, model 5). Capture probability was best described as varying by session. However, standard errors around parameter estimates were large for this model, so it

was excluded from the analysis. The next best supported model, with an additive effect of year and season, $p(\text{year}+\text{season})$, was selected to model p (Table 2-2, model 1).

To model Ψ , we investigated the best approach to modeling a breeding season effect on Ψ . Breeding seasons vary over the cotton rat's geographic range (Cameron and Spencer 1981, Whitaker and Hamilton 1998). In the southern part of the range, breeding occurs year round but with peaks at certain times of the year. Because a literature review did not give a clear indication of when peak seasons occur in southwestern Georgia, we created a model set, based on the literature (Cameron and Spencer 1981, Whitaker and Hamilton 1998) and personal observations, to identify peak and non-peak breeding seasons. This analysis indicated reproductive peaks in spring and summer (Table 2-1, model 1).

Because of potential confounding effects of prescribed burning treatments and breeding seasons occurring as occasion-dependant effects, we then assessed whether there was support for further dividing the non-breeding seasons (winter and fall) into whether a burn occurred during these seasons or not. Division of non-breeding seasons into two classes based on burning was well supported (Table 2-2, model 7).

Using this breeding season model (Table 2-2, model 7), we continued the sequential variable selection for Ψ as described above for p and S . Reproductive condition, sex, and breeding season, modeled in an additive fashion ($\Psi(\text{reproductive condition}+\text{sex}+\text{breeding season})$), were important for describing Ψ (Table 2-2, model 10).

Although the prescribed fires occurred at specific times, fire-caused changes in cover and food resources may last for weeks or months. To determine the best effect

window for the fire treatments, a set of models considering fire effects on survival over multiple time intervals was considered. Survival was constrained to be similar between all trapping periods except those following fires. Post-fire survival was allowed to vary for several different intervals, from including only the interval during which the fire occurred (interval length of ten weeks following the 2005 and 2007 fires and of five weeks following the 2009 fire), to including intervals through the summer season (30weeks), by which time vegetation is typically recovered. This analysis indicated a short term fire effect on survival with declines occurring only in the interval during which the fire occurred (Table 2-3, model 1).

Exclosure and control sites were initially selected as pairs based on similar habitats between pairs. As part of a post-hoc examination of non-treatment effects on S and Ψ , we examined the potential for paired site effects on these parameters. Using the base models indicated by the analyses described above, we ran a second set of models considering paired site effects on S and Ψ . This analysis indicated paired site effects were important for modeling both S and Ψ (Table 2-4, model 1).

Treatment effects were added to the best base multistate model ($S(\text{reproductive condition}*\text{sex}+\text{site})p(\text{year}+\text{season})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site}))$ as additive and interactive effects (two-way only). Due to confounding effects relating to fire and breeding season occurring as occasion-dependent effects, only food and predation treatments were considered with respect to Ψ while food, predation, and fire effects were considered with respect to S . Model averaging was employed to generate parameter estimates for S and Ψ .

Pollock's robust design (Pollock 1982) was used to generate abundance estimates (N). Robust design models estimate probabilities for survival (S), capture (p), recapture (c), emigration (γ''), and staying away after emigrating (γ'). The model selection approach used for the robust design was similar to that used for the multistate analysis. Preliminary investigation considered potential for time effects on p and c . Paired site effects were considered for N . S was modeled using the best supported S model from the multistate analysis (without reproductive condition, $S(\text{sex}+\text{site}+\text{food}+\text{fire})$). γ terms were modeled using a random emigration effect ($\gamma''(\cdot)=\gamma'(\cdot)$). Preliminary analyses indicated that c and p varied by trapping session (Table 2-5 model 3) and that a paired site effect, as described above, was important for modeling N (Table 2-5, model 1).

Because of the difficulties associated with modeling treatment effects on abundance directly (White 2002), the best supported robust design model indicated by the preliminary analysis described above ($S(\text{site}+\text{sex}+\text{food}+\text{fire})\gamma''(\cdot)=\gamma'(\cdot)p(\text{session})c(\text{session})N(\text{site})$) was used to generate derived abundance estimates by site and session, but not to determine treatment effects. Treatment effects on abundance were evaluated using a repeated measures ANOVA (Schabenberger and Pierce 2002) implemented using the PROC MIXED procedure in SAS (SAS Institute Inc. 2004). The model for this ANOVA included food, fire, and predation treatments and their interactions (two-way interactions only). Paired sites were included as a random effect. Multiple covariance structures were investigated and the best (variance components structure, which allows a different variance for each random effect) was selected based on AICc value (Miller et al. 2004). Treatment effects were considered significant at the $\alpha = 0.05$ level.

Survival analysis using radio telemetry data

Survival of collared rats was estimated using the Cox proportional hazard model (Cox 1972) implemented using the PROC PHREG procedure in SAS (Allison 1995). An a priori model set was constructed to examine the effects of season, treatment, sex, and interactions of these factors on survival. Rats that lived less than one week following collaring or that died due to handling-related causes were not considered for this analysis. To prevent an upward bias associated the censoring of rats in the latter group, the first week of all rats was censored as well. Rats whose signals were lost and rats who lost collars were right-censored. Seasons were pooled except for winters which were separated into winter 2008 (no burning) and winter 2009 (burning occurred) to test for a fire effect on survival. Models were assessed using an AIC framework.

Home range analysis

Home ranges were estimated using 95% minimum convex polygons (MCP) and, for purpose of comparison to other studies, 95% fixed kernel methods. To avoid short sampling intervals and small sample sizes which may contribute to inaccurate home range estimates (Swihart and Slade 1985a, Swihart and Slade 1985b, Spencer et al. 1990), we followed the recommendations of Cameron and Spencer (1985) and Swihart and Slade (1985b) and estimated home ranges only for rats that had a minimum of 15 locations with least 4.5 hours between locations. MCP estimates were generated using the program CALHOME (Kie et al. 1994). Kernel estimates were generated in ArcGIS 9 (ESRI 2005) using the Hawth's tools extension (Beyer 2004). Kernel bandwidth was specified by least squares cross validation (LSCV, Seaman and Powell 1996) for all rats, with the exception of nine rats that were repeatedly found at the same location(s) (usually a nest or burrow). For these rats, the bandwidth was user specified to prevent

bias such behavior can create in home range estimates using LSCV to determine bandwidth (Seaman and Powell 1996). Home range estimates were annual, not seasonal (although “annual” is perhaps misleading as no rats lived to be collared for more than a year).

A *t*-test indicated that male rats had significantly larger home ranges than females; therefore, males and females were considered separately in further analysis. Effects of feeding, predation and the interaction of these treatments on home range size were examined using a two-way ANOVA (SAS procedure PROC GLM, SAS Institute Inc. 2004, Schabenberger and Pierce 2002). Fire was not included as a treatment in this analysis due to small post-fire sample sizes.

Home range exclusivity was estimated by identifying all pairs of rats that lived during the same period and which had adjacent or overlapping MCP home ranges. Distances between pairs of such individuals located by radio telemetry within thirty minutes of each other were measured in ArcGIS 9. Distances between randomly selected locations for each pair were also measured. Averaged distances were subtracted (average real – average random distance) for each pair to generate an estimate of exclusivity. Positive differences are interpreted to indicate a pair’s avoidance of each other, while negative differences indicate an affinity. Effects of treatments on this measure were examined using a two-way ANOVA implemented in PROC GLM in SAS. Independent variables included in these models were type of pairing (male/male, female/female, male/female), feeding treatment, predation treatment, and interactions of type of pairing with feeding and predation treatments

(two-way interactions only). Fire was not included as a treatment due to small post-fire sample sizes.

Results

CMR Analyses

Over 26 trapping sessions in eight trapping plots, 2557 individual cotton rats (6815 total captures) were trapped. The multistate analysis results show six models with a $\Delta QAI Cc < 2$, none with particularly strong support over the others (Table 2-6). It is clear from the top ranked models that fire and supplemental feeding effects were important factors affecting survival. Fire effects appear in the top 30 models and these hold 100% of the model weight of the set. Food effects appear in the top 14 models and these carry 92.5% of the model set's weight. There is no evidence that supplemental food or predator exclusion treatments influenced Ψ . The lack of clear support for any particular model indicates model selection uncertainty; therefore, model averaging was employed for parameter estimation.

Overall model averaged survival estimates showed that males had lower survival than females and that reproductive individuals had lower survival than non-reproductive individuals (Figure 2-1). Model averaged estimates show large post-fire declines in survival for both sexes and strata in both the predator exclosures and controls (Figure 2-1). Post-fire survival was not greatly impacted by the addition of food and still approached zero. During non-fire periods, food supplementation increased survival for both sexes and reproductive conditions (Figure 2-1). Survival was greater in predator exclosures compared to controls, but this difference was marginal. Similarly, predator exclusion conveyed some benefit to survival post-fire, but this was small in magnitude (Figure 2-1).

Model averaged estimates of Ψ show that a greater proportion of males made transitions into reproductive states than females in all seasons (Figure 2-2). Additionally, most reproductive individuals that achieved a reproductive state stayed in a reproductive state; this trend was slightly greater for males than females (Figure 2-2).

Initial investigation indicated a strong fire effect on transitions between reproductive states: models that included three classes of breeding seasons (peaks in spring and summer, non-peak breeding in falls and winters without burns, and a second non-peak in falls and winters with burns; hereafter peak, non-peak/non-burn, and non-peak/burn, respectively) were clearly better supported than models with only two classes of breeding seasons (peak and non-peak with no distinguishing between burn and non-burn years, Table 2-1). Two-season breeding season models had no support (weight = 0.0) compared to three-season models (Table 2-1, model 7).

Model averaged parameter estimates indicated that transitions to reproductive states were at their highest during peak breeding seasons but that there was only a small drop in transitions to reproductive states during non-peak/non-fire seasons (Figure 2-2). However, transitions to reproductive states dropped considerably during non-peak/fire seasons (Figure 2-2). Addition of food increased transitions to reproductive states while predator exclusion had a minimal effect on this parameter (Figure 2-2).

The repeated measures ANOVA examining treatment effects on abundance indicated significant effects of feeding and fire treatments and their interaction ($P = 0.001$, $P < 0.001$, and $P = 0.045$ respectively). Examination of least square means showed that supplemental feeding increased abundances by 1.9 times and burning

caused a 3 fold decline in abundance. Although the interaction of feeding and burning was marginally significant, burning in feeding areas still produced large declines in abundance (by 2.9 times) indicating that this interaction is not biologically significant.

Analyses of Radio Telemetry Data

A total of 279 cotton rats were collared during this study. Of these, 145 had sufficient locations for home range and exclusivity analysis; 204 met criteria for survival analysis. The average number of locations per home range (\pm SE) was 29.83 ± 1.29 (range 15-92). Male home ranges were significantly larger than female home ranges ($P < 0.001$). Average home range size was 2948 m^2 (range 685-9814 m^2) for female rats ($N = 72$) using MCP and 5983 m^2 (range 888-20917 m^2) using fixed kernel methods. For males ($N = 73$) the average home ranges were 7891.5 m^2 (range 150-30590 m^2) and 15845.31 m^2 (range 511-84248 m^2) using MCP and kernel methods. Although kernel estimates were substantially larger than MCP estimates, results from the two methods did not differ qualitatively. Overall, we believe the 95% MCP estimates provide a more accurate picture of actual space use, and include kernel estimates here for comparison purposes; therefore, the discussion will primarily focus on results based on the MCP home range estimates.

Collared rat survival

Of the 204 rats that met criteria for survival analysis, 29 were censored for at least some time during which they were not tracked (slipped/chewed off collar, or experienced transmitter failure), but were recollared and reentered into the analysis at some later point. Sixty-two rats were censored and never reentered into analysis. Causes for censoring included slipping/chewing off collars ($N = 21$), emigrating from the control/exclosure plot where collared ($N = 13$), transmitter failure ($N = 2$), and

unexplained loss of the signal (N = 26). The latter could be attributed to transmitter failure, emigration, or carrying off of the rat and/or collar by a far-ranging predator.

There was strong evidence for seasonal and fire effects on survival of collared rats (Table 2-7). Models including only spring, summer, and fall effects (models 8, 9, and 11, Table 2-7) show that spring, summer, and fall survivals were similar (had AICc values within a range of 2) while survivals during winters where burning occurred and during winters where burning did not occur differed from each other and from other seasons (AICc values >2 from other seasonal models). Parameter estimates from the top ranked model (Table 2-7, model 1; survival varying by season), show that winter survival in non-burn years was greater than other seasons, while survival in winters of burn years was quite low (Figure 2-3).

There was poor support for supplemental feeding and predation treatment effects on collared rat survival; the highest ranked model with a treatment term has moderate support ($\Delta\text{AICc} = 4.14$, Table 2-7, model 3)). This model indicated an interactive effect of season with the predator exclusion treatment. Parameter estimates from this model show that survival was similar between controls and exclosures for all seasons except winters of burn years, during which time survival was lower in predator controls than exclosures (Figure 3-3).

Effects on home range size

The only significant treatment effect on home ranges estimated by MCP was for male rats in the predator treatment (Table 2-8). Examination of least square means showed that males in the predator exclosures had larger home ranges than males in the predator controls ($P = 0.001$). Neither feeding nor interactions of feeding and predator

treatments had significant effects on home range size. Similar results were found when examining kernel home range estimates.

There was no evidence that feeding or predator exclusion treatments, or their interaction, had significant effects on female home ranges estimated by MCP (Table 2-8). Similar tests performed using kernel estimates showed a marginally significant predation effect (again, larger home ranges in exclosures, $P = 0.048$), while feeding and the interaction of feeding and predation treatments showed no significant effects.

Effects on home range exclusivity

Three hundred and fifty-six pairs of rats had adjacent or overlapping home ranges during the same time period. Analysis of home range exclusivity suggested no effect of type of pair or treatment on spacing between rats (Tables 2-9 and 2-10).

Effects of fire on radio collared rats

Thirty-three collared rats were collared and tracked during the February 2009 burns. All rats survived the fire itself by sheltering in holes within their home ranges or nearby areas that did not burn completely. Forty-one percent of the rats died due to predation, 34% emigrated to small, unburned patches within the larger burn area and 19% emigrated to unburned areas completely outside of the burn unit. All but one rat either died or emigrated within seven days of the fire (this rat died twelve days post-fire). Predation and feeding treatments did not significantly affect response to fire ($P > 0.05$).

Of the remaining two rats, one chewed its collar off in a hole in the burn area; the other stayed within the burn area (an unfed predator exclosure) and apparently died due to starvation. This rat was found near the entrance of a hole within its home range seven days post-fire. A necropsy revealed that the rat had lost 19% of her body weight

since she was last trapped (34 days prior). There were no signs of trauma commonly apparent following mammalian, avian, or snake predation/attempted predation. The stomach contained primarily ash and dirt. Two rats killed and cached by mammalian predators in a fed/predator access grid during the same period were also necropsied to reveal stomachs filled with rabbit chow, indicating the individuals in fed grids used supplemental food following the fire.

Every rat that moved to an unburned patch within the larger burn area moved less than 50 m. These unburned patches overlapped or were adjacent to the rats' pre-fire home ranges; it is likely the rats were already familiar with the unburned patches they invaded. Six of these rats survived and were captured during the next trapping period. Five had lost weight during this interval. The mean percent weight loss was -0.083% over 33 days. To determine if this was an artifact of the winter season itself, weight changes of collared rats over the 2008 winter were also calculated. Of 9 collared rats which were captured in both winter 2008 sessions (35 days between sessions), the mean weight change was a gain of 0.082% . Change in weight differed ($P = 0.003$) between winter of 2008 and 2009.

Of rats that successfully emigrated to areas outside of the burn unit, most did so in a single night and moved distances of 50 to 700 m. None appeared to have moved the shortest distance to the burn edge and/or stopped immediately upon reaching an unburned area. Most of these rats (all but two) died or went missing within two weeks of emigrating.

Discussion

Fire Effects

Of the three treatments experimentally applied to cotton rat populations in this study (mammalian predator exclusion, supplemental feeding, and prescribed fire), fire had the largest impact on cotton rat populations. Prescribed burning caused precipitous declines in survival, abundance, and transitions to reproductive states regardless of the presence of supplemental food or absence of mammalian predators. These results support the hypothesis that cotton rat declines following fires are due primarily to predation, secondarily to emigration, and not due to changes in food resource availability. However, one radio collared rat apparently died of starvation following a burn and other rats that remained in small, unburned patches in the overall burn unit lost a significant amount of weight. This suggests that the loss of herbaceous food sources by burning was indeed a problem for this species, but that the crisis of food resources was overwhelmed by increased exposure to predators due to loss of cover. This is not surprising given the cotton rat's heavy cover requirements and general susceptibility to predation; cotton rats support a wide variety of predators including snake, mammalian, and avian predators. Predation is by far the most common cause of death (82% of deaths, Derrick 2007, and here, 76% of collared rat deaths overall) and cotton rat populations can experience near complete turnover in as little as five to eight months (Goertz 1964).

These results suggest that in ecosystems where fires are frequent, such as longleaf pine, cotton rat populations are heavily influenced by fire events. Similar sharp post-fire declines in cotton rat abundances have been observed in southern pine forests, native tallgrass prairies, and sacaton grasslands (Arata 1959, Layne 1974, Bock

and Bock 1978, Rehmeier et al. 2005). Although cotton rats experience a short-term negative fire effect, over the long term cotton rats have a positive association with fire. Populations in tallgrass prairies in Kansas peaked in autumns of the first two years following spring burns but declined in autumns thereafter if burns were not repeated (Rehmeier et al. 2005). Rehmeier et al. (2005) hypothesize that this occurs because fires enhance growth of plants that serve as food resources and reduce litter that may inhibit movement through vegetation.

Predation and Supplemental Feeding Effects

Given that population dynamics of species such as cotton rats with rapid maturation and turnover are more sensitive to changes in reproductive parameters than to changes in survival (Heppell et al. 2000, Oli and Dobson 2003), it is somewhat surprising that we found no strong evidence of predator or feeding treatment effects on reproductive transitions but did observe increased survival in supplemental feeding plots. This may be explained by canalization of vital rates which have great proportional impact on population growth rate; such rates tend to have little variation due to heavy selective pressure on those parameters (Pfister 1998) and are unlikely to be greatly affected by environmental changes.

Cotton rats are extraordinary reproducers even when compared with other rat species. Cotton rats become reproductive within one to two months, require 27 days for gestation, and a female may become pregnant again within 24 hours of giving birth (Whitaker and Hamilton 1998). Young open eyes within 24 hours, wean at five to six days, and achieve independence soon after. By contrast, Norway rats (*Rattus norvegicus*) open eyes at 14 to 17 days, wean at three weeks and become independent at four weeks (Whitaker and Hamilton 1998). Given the cotton rat's already accelerated

schedule of development and reproduction, it is difficult to imagine there is much room for improvement. A similar study on effects of supplemental feeding on cotton rats found that feeding increased the number and weight of young born in feeding plots but did not affect juvenile survival or recruitment (Campbell and Slade 1995).

The lack of predation effects observed here is also surprising given the enormous role predation plays in cotton rat mortality. It is possible that mammalian predator exclusion alone was insufficient to elicit a response in the parameters examined. Previous studies examining predator exclusion or removal on cotton rats (Weigert 1972, Guthery and Beasom 1977) suggest that the effects of such treatments vary according to the predators excluded or removed. Guthery and Beasom (1977) removed only mammalian predators from areas where cotton rats occurred, and detected no change in survival or density. Weigert (1972) excluded all predators from some study areas and only mammalian predators from others and determined that avian predators had a greater impact on cotton rat populations than mammalian predators. These results are consistent with our own which suggest that predation by raptors and snakes make up for losses when mammalian predators are excluded. Alternatively, it is possible that predation does not regulate cotton rat populations in areas or periods where cover is sufficient. This hypothesis is supported by the positive supplemental feeding effect (increased survival, abundance, and transitions to reproductive states) observed during non-fire periods.

Although we did not observe strong predation effects on survival, abundance, or reproductive transitions, predator exclusion was associated with increased male home range sizes. This indicates a sub-lethal predation effect. The best studied examples of

sub-lethal effects of predation deal with the interplay of food acquisition and predation risk. Foraging increases exposure to predators, causing individuals to make trade-offs between the need to eat and the need to minimize predation risk (McNamara and Houston 1987, Abrams 1991). The lack of feeding effects on home range size suggests that cotton rats do not make such trade-offs, at least with respect to mammalian predation. Instead, we found that male rats made trade-offs associated with predator exclusion alone. How can this be explained outside of a food context? Given the previously stated importance of reproduction over survival in species that have rapid turnover and maturation (Oli and Dobson 2003), it follows that male rats, who are promiscuous, range widely, and have no involvement in raising young would make predation risk decisions based on maximizing reproductive opportunities rather than food acquisition. That the same trend was not observed with female rats can be explained by the likelihood that a female rat will be bred regardless of whether she encounters a single male or several. While female rats are less likely to influence reproduction by changing space use, male rats ought to increase fitness by mating with as many females as possible. Maintenance of larger home ranges should increase the chances of encountering females and the chances of breeding. However, when predation pressure is high, maintaining a large home range may increase predation risk causing male rats to restrict movements.

Although we did not detect a strong predation treatment effect on survival of trapped rats, we found that radio collared rats had greater survival in controls than exclosures in winters during which burning occurred (compared to winters where burning did not occur, during which survival was similar between predator controls and

enclosures). This may indicate additional support for sub-lethal effects of predation, but we believe it to be due instead to site effects. Specifically, one section of the unfed predator control which contained collared rats did not burn completely. Six collared rats had home ranges adjacent to this area and, by moving into the area, which provided cover, were less vulnerable to predation. Given that these six rats made up a significant portion of rats in predator control treatments during the burn (N = 18), it is possible that this skewed the results relating to post-fire predation treatment effects on collared rat survival. If it were not for this, we believe these results would have been similar to those observed from the CMR analyses: fire caused a decline in survival and that decline was not affected by the predation treatment. However, these results indicate that the negative short-term fire effect can be mitigated if unburned refugia remain (although rats seemed unable to reliably find such refugia if it occurred at distances greater than 50 to 70 m from their home ranges).

Home Range Exclusivity

Although our analysis failed to detect a treatment effect on cotton rat home range exclusivity, it is interesting that previous studies have found that female cotton rats have more exclusive home ranges than males and that heavier males have more exclusive ranges than smaller males (Fleharty and Mares 1973, Cameron and Spencer 1985). We found no significant differences in exclusivities between male and female rats or between rats in any treatment. The inconsistency in these results may be due to different methodologies used to quantify home range exclusivity. Cameron and Spencer (1985) estimated overlap for co-occurring rats tracked by radio telemetry around sun rise and sunset by calculating percent overlap of MCP home ranges. Fleharty and Mares (1973) also examined overlap and distances between centers of

activity of individuals, although these estimates were based on home ranges generated with as few as six trapping locations.

We used a different method to evaluate the tolerance of cotton rats for each other. Locations were taken by radio telemetry at all times between dawn and dusk, and exclusivity was evaluated by comparing distances between co-occurring individuals tracked at the same time to random distances between those individuals. Given the social system of cotton rats, this may provide a more accurate means of evaluating interactions between rats. Liu (1971) found in a large-scale laboratory study that cotton rat populations consist of dominant and subordinate individuals (defined by whether an individual wins or loses fights – submissive behavior was not observed). Subordinate individuals lived within home ranges of dominant individuals but minimized encounters by foraging at less desirable times; dominant individuals foraged around dawn and dusk while subordinates foraged during day or night hours. Subordinate rats defended only areas immediately around their nests. Dominant rats tended not to have overlapping home ranges with other dominant rats as encounters between two dominants generally ended with the death of one rat or the other. Mating pairs shared nests at times, although they did not forage together, and females moved to new nests which were defended even from her mate shortly before giving birth and while nursing young.

Since cotton rats use extensively overlapping areas, measuring home range overlap provides limited insight into territoriality, especially for home ranges generated from points collected at times when only a subset of the population is likely to have been active. The exclusivity measure used here allows an indirect examination of

tolerance of cotton rats for each other in a system where individuals use the same space but are solitary and agonistic towards one another.

Other studies have found that rodents decrease agonistic behavior when provided supplemental food, but not with respect to predation pressure (Desy et al. 1990). We were unable to detect changes in tolerance of rats towards each other with predation or feeding treatments. It is possible that the food provided was insufficient or too greatly dispersed to allow a decrease in aggression and that the presence of avian and snake predators prevented behavioral responses at this level to mammalian predator exclusion.

Conclusions

Our results suggest that cotton rat population dynamics in our study site are primarily driven by fire events. Population responses following fires appear to be strongly influenced by fire-caused loss of cover and associated increases in predation. Direct effects relating to mammalian predation do not appear to be strong, but there is evidence that male cotton rats respond adaptively to predation risk, by decreasing home range size in areas where mammalian predators have access compared to areas where they do not. Food is also important to cotton rats, and caused increases in all of the demographic parameters considered here. This is likely to be true in both fire and non-fire periods, but food effects were overwhelmed by predation effects following fires. We detected no treatment effects on cotton rat behavior associated with spacing between individuals.

Table 2-1. Model comparison table for multistate capture-mark-recapture analysis assessing occurrence of peak breeding seasons of cotton rats in general (Model set 1) and with respect to winter prescribed burns (Model set 2) in Southwestern Georgia between 2005 and 2009. All models had survival set as $S(\text{reproductive condition} \times \text{sex})$ and capture probability set as $p(\text{year} + \text{season})$. Table includes number of parameters (K), model weights (relative likelihood of models in the set), and difference in Akaike's information criterion corrected for small sample size after quasiliikelihood adjustment (ΔQAICc). Quasiliikelihood adjustments were made using an estimated \hat{c} of 1.262.

	Model no.	Model	K	ΔQAICc	Model weight
Model set 1*	1	$\Psi(\text{spring and summer peaks})$	15	0.00	1.00
	2	$\Psi(\text{spring peaks})$	15	80.92	0.00
	3	$\Psi(\text{summer and fall peaks})$	15	103.07	0.00
	4	$\Psi(\text{summer peaks})$	15	110.02	0.00
	5	$\Psi(\text{dot})$	14	148.42	0.00
	6	$\Psi(\text{spring, fall, and summer peaks})$	15	150.39	0.00
Model set 2**	7	$\Psi(\text{spring and summer peaks; winter and fall non-peaks divided by years and non-burn years})$	16	0.00	1.00
	8	$\Psi(\text{spring and summer peaks; winter and fall non-peaks})$	15	74.08	0.00

* Model set 1 considers only two classes of breeding season: peak (listed) and non-peak (all seasons not listed for a given model).

** Model set 2 compares the best model from set 1 (model number 1) with a similar model that considers three classes of breeding seasons by breaking down non-peak seasons into those that occurred during burn years (winters and falls of 2005, 2007, and 2009; burns occurred in winters of these years) and those that occurred during non-burn years (winters and falls of 2006 and 2008).

Table 2-2. Model comparison table for multistate capture-mark-recapture analysis assessing sex, reproductive condition, breeding season and time effects on capture probability (p), survival (S), and rates of transitions between reproductive states (Ψ) in cotton rats in Southwestern Georgia between 2005 and 2009. See Table 2-1 for column definitions.

Model no.	Model	K	$\Delta QAI C_c$	Model weight
Effects on capture probability (p) *				
1	$p(\text{year}+\text{season})$	18	0.00	1.00
2	$p(\text{season})$	14	20.79	0.00
3	$p(\text{year})$	14	83.26	0.00
4	$p(\text{constant})$	10	124.66	0.00
Effects on survival (S)**				
5	$S(\text{reproductive condition}*\text{sex})$	34	0.00	1.00
6	$S(\text{sex})$	32	11.18	0.00
7	$S(\text{reproductive condition}+\text{sex})$	33	13.10	0.00
8	$S(\text{constant})$	31	21.63	0.00
9	$S(\text{reproductive condition})$	32	23.00	0.00
Effects on rates of transitions to reproductive states***				
10	$\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	34	0.00	1.00
11	$\Psi(\text{breeding season}+\text{reproductive condition})$	33	16.72	0.00
12	$\Psi(\text{breeding season})$	32	95.93	0.00
13	$\Psi(\text{breeding season}+\text{sex})$	33	102.04	0.00
14	$\Psi(\text{constant})$	30	324.08	0.00

* Additional parameters modeled as $S(\text{reproductive condition}*\text{sex})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

** Additional parameters modeled as $p(\text{session})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

*** Additional parameters modeled as $S(\text{reproductive condition}*\text{sex})p(\text{session})$.

Table 2-3. Model comparison table for multistate capture-mark-recapture analysis assessing the term of effect of winter prescribed burns on survival (S) of cotton rats in Southwestern Georgia between 2005 and 2009. See Table 2-1 for column definitions. All models had additional parameters of capture probability (p) modeled as $p(\text{year}+\text{season})$ and rate of transition between reproductive states (Ψ) modeled as $\Psi(\text{reproductive condition}+\text{sex}+\text{breeding season})$.

Model no.	Model	K	ΔQAICc	Model weight
1	S(fire effect over 5 (2009) to 10 weeks (2005 and 2007))*	16	0.00	0.98
2	S(fire effect over 30 weeks)	16	7.85	0.02
3	S(fire effect over 10 weeks)	16	15.72	0.00
4	S(fire effect over 20 weeks)	16	21.32	0.00

* Model 1 shows a range of intervals because the interval between trapping sessions changed from 10 weeks (2005 and 2007) to 5 weeks (2009) before the 2009 prescribed burn.

Table 2-4. Model comparison table for multistate capture-mark-recapture analysis assessing potential for paired site effects on survival (S) and rate of transitions to reproductive states (Ψ) of cotton rats in Southwestern Georgia between 2005 and 2009. See Table 2-1 for column definitions. All models had capture probability (p) modeled as $p(\text{year}+\text{season})$.

Model no.	Model	K	ΔQAICc	Model weight
1	$S(\text{reproductive condition}*\text{sex}+\text{site})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site})$	24	0.00	0.84
2	$S(\text{reproductive condition}*\text{sex}+\text{site})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	21	3.26	0.16
3	$S(\text{reproductive condition}*\text{sex})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site})$	21	21.70	0.00
4	$S(\text{reproductive condition}*\text{sex})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	18	25.08	0.00

Table 2-5. Model comparison table for robust design capture-mark-recapture analysis assessing demographic and time effects on abundance (N), capture probability (p), and recapture probability (c) in cotton rats in Southwestern Georgia between 2005 and 2009. See Table 2-1 for column definitions. Survival (S) was modeled as $S(\text{site}+\text{sex}+\text{food}+\text{fire})$ for all models. Emigration terms (γ'' and γ') were modeled with a random emigration effect for all models: $\gamma''(\cdot)=\gamma'(\cdot)$.

Model no.	Model	K	ΔAICc	Model weight
Effects on abundance (N)*				
1	$N(\text{site})$	64	0.00	1.00
2	$N(\cdot)$	61	119.80	0.00
Effects on capture (p) and recapture (c) probabilities**				
3	$p(\text{session})c(\text{session})$	64	0.00	1.00
4	$p(\text{session})c(p+c')^{***}$	39	35.02	0.00
5	$p(\cdot)c(p+c')^{****}$	14	538941.84	0.00

*Additional parameters were modeled as $p(\text{session})c(\text{session})$. **Additional parameter was modeled as $N(\text{site})$.

***Indicates capture probability varies by session with a constant trap happy response recapture response (c').

****Indicates a constant capture probability with a constant trap-happy recapture response (c').

Table 2-6. Model comparison table for multistate capture-mark-recapture analysis examining the effect of predation, supplemental feeding, and fire treatments on survival (S) and transition probabilities (Ψ , between reproductive and non-reproductive states) of cotton rats in Southwestern Georgia between 2005 and 2009. Capture probability modeled was modeled as p(year+season) for all models. See Table 2-1 for column definitions. Bolded text indicates treatment effects (all other effects are similar between models throughout the set). Only models with a $\Delta QAI Cc < 4$ are shown here (the top ranked 12 models of 55 in the overall set).

Model no.	Model	K	$\Delta QAI Cc$	Model weight
1	S(reproductive condition*sex+site+ food*fire) Ψ (breeding season+reproductive condition+site+sex)	27	0.00	0.16
2	S(reproductive condition*sex+site+ food*fire) Ψ (breeding season+reproductive condition+site+sex+ food)	28	0.11	0.16
3	S(reproductive condition*sex+site+ food+predation+fire) Ψ (breeding season+reproductive condition+site+sex)	27	0.93	0.10
4	S(reproductive condition*sex+site+ food+predation+fire) Ψ (breeding season+reproductive condition+site+sex+ food)	28	1.05	0.10
5	S(reproductive condition*sex+site+ food+fire) Ψ (breeding season+reproductive condition+site+sex)	26	1.79	0.07
6	S(reproductive condition*sex+site+ food+fire) Ψ (breeding season+reproductive condition+site+sex+ food)	27	1.90	0.06
7	S(reproductive condition*sex+site+ food*fire) Ψ (breeding season+reproductive condition+site+sex+ predation)	28	2.03	0.06
8	S(reproductive condition*sex+site+ food*fire) Ψ (breeding season+reproductive condition+site+sex+ food+predation)	29	2.13	0.06
9	S(reproductive condition*sex+site+ food+predation+fire) Ψ (breeding season+reproductive condition+site+sex+ predation)	28	2.96	0.04
10	S(reproductive condition*sex+site+ food+predation+fire) Ψ (breeding season+reproductive condition+site+sex+ food+predation)	29	3.06	0.04
11	S(reproductive condition*sex+site+ food+fire) Ψ (breeding season+reproductive condition+site+sex+ predation)	27	3.82	0.03
12	S(reproductive condition*sex+site+ food+fire) Ψ (breeding season+reproductive condition+site+sex+ food+predation)	29	3.91	0.02

Table 2-7. Factors influencing survival of radio collared cotton rats in sites treated with supplemental feeding, winter prescribed fires, and mammalian predator exclusion in southwestern Georgia from June 2007 – August 2009. Models and associated AICc rankings and weights for collared rat survival were estimated using Cox proportional hazard models. See Table 2-1 for column definitions. “Winter (non-burn)” refers to the winter of 2008 during which no sites were burned. “|” notation indicates that all additive and interaction combinations of variables are included in the model. “|” notation indicates that all additive and interaction combinations of variables are included in the model.

Model no.	Model	K	Δ AICc	Model weight
1	Season	5	0.00	0.57
2	Winter (burn)*	2	1.21	0.31
3	Predation season	12	4.14	0.07
4	Food season	12	6.67	0.02
5	Winter (non-burn)	2	7.88	0.01
6	Sex season	12	9.56	0.01
7	Constant survival	1	13.65	0.00
8	Spring	2	13.72	0.00
9	Summer	2	14.74	0.00
10	Predation	2	14.84	0.00
11	Fall	2	14.92	0.00
12	Food	2	15.24	0.00
13	Sex	2	15.58	0.00
14	Food sex	4	17.42	0.00
15	Predation sex	4	17.84	0.00
16	Predation food	4	18.23	0.00
17	Global model	27	26.24	0.00

* Winter (burn) refers to the winter of 2009 during which all sites were treated with prescribed fire.

** Winter (non-burn) refers to the winter of 2008 during which no sites were burned.

Table 2-8. Factors influencing home range size of cotton rats in southwestern Georgia using 95% minimum convex polygon (MCP) and 95% fixed kernel (Kernel) estimates. General linear model results are given with interactive effects. Degrees of freedom (*d.f.*), mean square (MS), *F*-statistic values (*F*), and significance level (*P*) are given for each effect. Home ranges were log transformed for this analysis.

Method					
	Source	<i>d.f.</i>	MS	<i>F</i>	<i>P</i>
Male rats MCP	Food	1	0.055	0.40	0.559
	Predation	1	1.768	11.020	0.001
	Food*Predation	1	0.008	0.050	0.822
Kernel	Food	1	0.023	0.17	0.685
	Predation	1	2.284	16.85	<0.001
	Food*Predation	1	0.003	0.02	0.879
Female rats MCP	Food	1	0.023	0.29	0.592
	Predation	1	0.147	1.85	0.178
	Food*Predation	1	0.111	1.39	0.242
Kernel	Food	1	0.036	0.44	0.509
	Predation	1	0.329	4.04	0.048
	Food*Predation	1	0.161	1.98	0.164

Table 2-9. Home range exclusivities for cotton rats in sites treated with supplemental feeding and mammalian predator exclusion in southwestern Georgia from June 2007 to August 2009.

Pair type	Treatment	N	Mean difference (m)*
Female/Female	Feeding	9	-1.80±2.08
	Non-feeding	21	-4.22±2.23
	Predator access	16	-5.14±2.69
	Predator exclosure	14	-1.62±1.84
Male/Male	Feeding	32	1.45±3.30
	Non-feeding	25	-2.24±2.46
	Predator access	27	1.00±2.79
	Predator exclosure	30	-1.21±3.23
Male/Female	Feeding	42	-2.50±1.59
	Non-feeding	49	2.05±1.85
	Predator access	49	-0.83±1.86
	Predator exclosure	42	0.87±1.65

* Exclusivity was estimated by finding actual distances between rats with adjacent minimum convex polygon home ranges that lived during the same time on days that they were located within 30 minutes of each other by radio telemetry. Random distances between each pair were also found. Mean difference is the mean of actual distances – random distances (±SE).

Table 2-10. Factors influencing home range exclusivities of cotton rats in sites treated with supplemental feeding and mammalian predator exclusion in southwestern Georgia from June 2007 to August 2009. General linear model results are given with interactive effects. Pair type refers to whether pairs were female/female, male/male, or male/female. See Table 2-4 for column definitions.

Source	<i>d.f.</i>	MS	<i>F</i>	<i>P</i>
Pair type	2	82.190	0.48	0.620
Food	1	9.289	0.05	0.816
Predation	1	17.267	0.10	0.751
Type*Food	2	347.416	2.03	0.135
Type*Predation	2	120.604	0.70	0.496

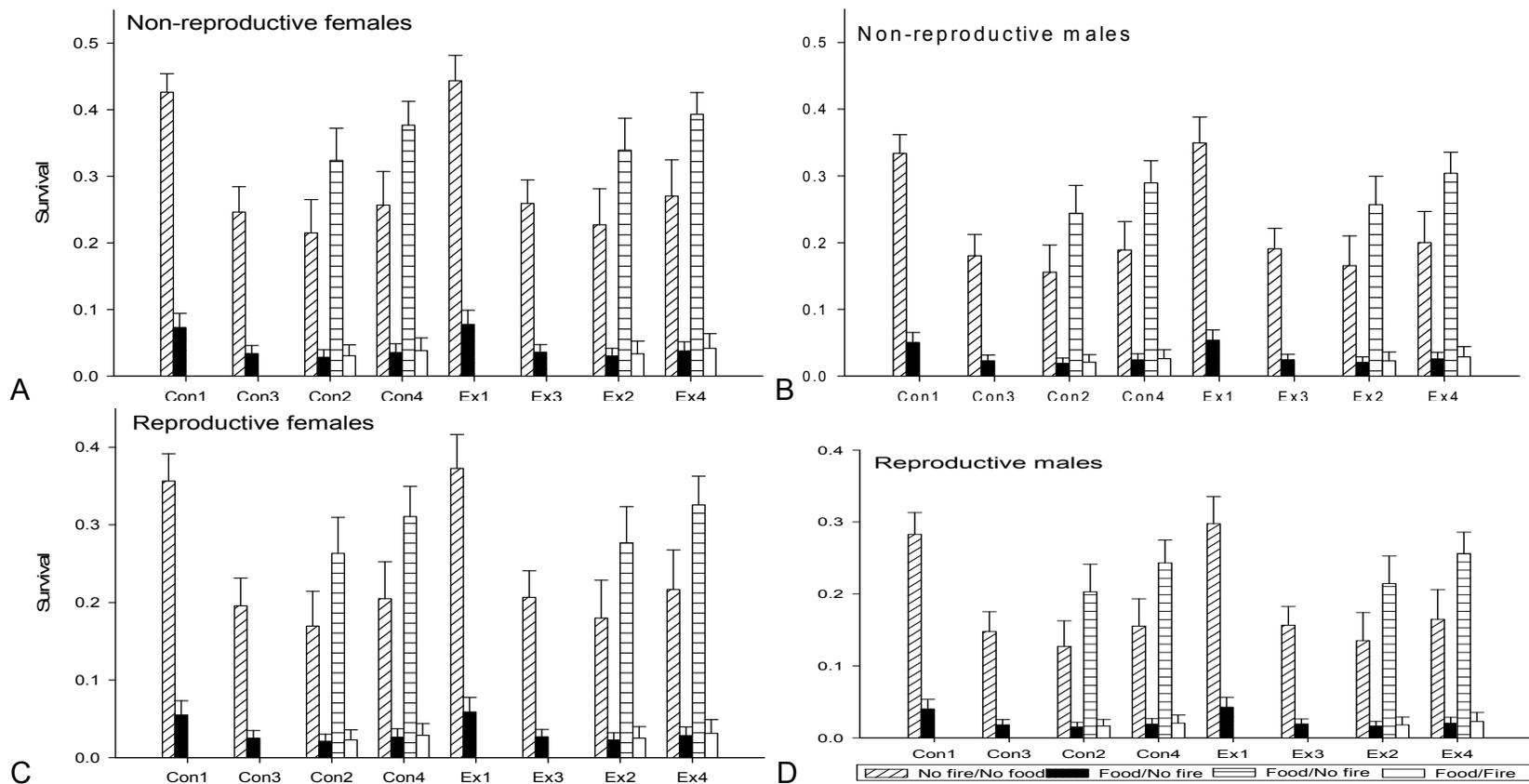


Figure 2-1. Model averaged estimates of survival of cotton rats in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and predator control treatments. Estimates are given for non-reproductive (A and B) and reproductive (C and D) male and female rats. Survival is estimated over 10 week intervals. Estimates are given by site: “Ex” sites refer to areas treated with mammalian predator exclusion while “Con” sites refer to areas where mammalian predators were allowed access. Supplemental feeding treatments were added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

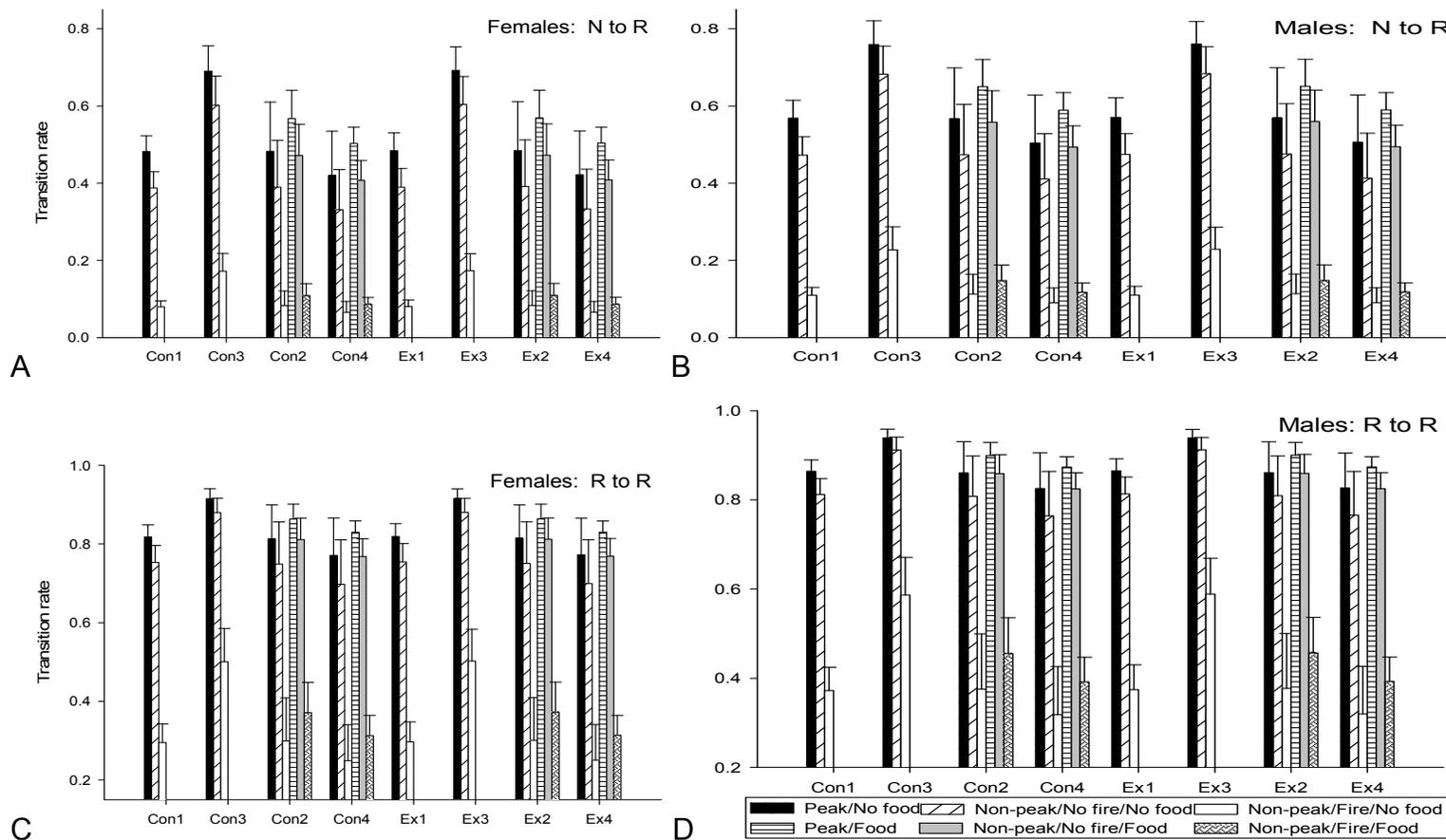
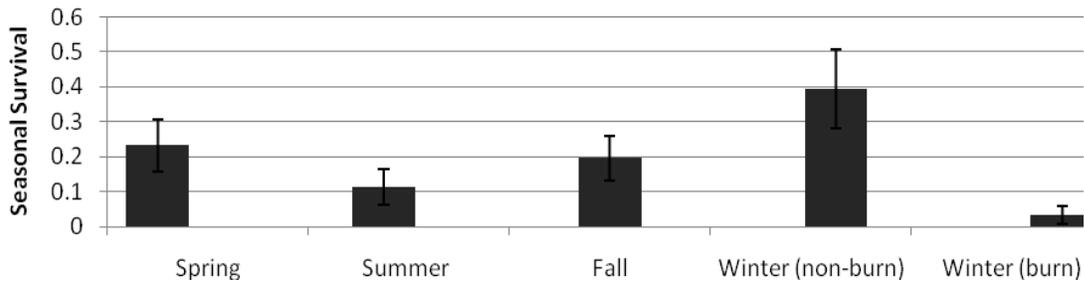


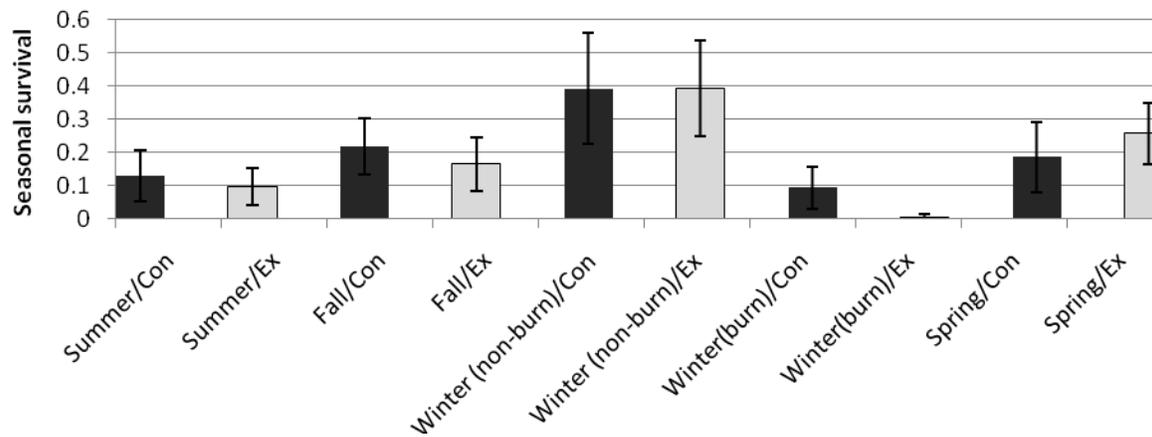
Figure 2-2. Model averaged estimates of the rates of transitions to reproductive states for male and female cotton rats during peak breeding seasons (spring and summer), non-peak seasons during which burning did not occur, and non-peak seasons during which burning did occur, in southwestern Georgia between 2005 and 2009. Transitions include movement of individuals from non-reproductive to reproductive states (N to R; A and B), and reproductive individuals staying in a reproductive state (R to R; C and D). Transitions occurred over 10 week intervals. Estimates are given by site: “Ex” sites refer to areas treated with mammalian predator exclusion and “Con” refers to mammalian predator access areas sites. Supplemental food was added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

Survival by season



A

Survival by season and predation treatment



B

Figure 2- 3. Survival estimates (\pm standard error) of radio collared cotton rats in southwestern Georgia between 2007 and 2009, generated using Cox proportional hazard models. Estimates for part A were generated using a model where survival varied by season (Table 7, model 1). Estimates for part B were generated using a model where survival varied by season and predation treatment (Table 7, model 3). Estimates are given by season and site: “Ex” sites refer to areas treated with mammalian predator exclusion while “Con” sites refer to areas where mammalian predators were allowed access. “Winter (burn)” refers to the winter of 2009 during which all sites underwent a prescribed burn. “Winter (non-burn)” refers to the winter 2008 during which prescribed burns were not carried out.

CHAPTER 3
EFFECTS OF SUPPLEMENTAL FEEDING, MAMMALIAN PREDATOR EXCLUSION,
AND PRESCRIBED FIRE ON COTTON AND OLDFIELD MOUSE POPULATIONS IN A
LONGLEAF PINE ECOSYSTEM

Introduction

Factors which limit populations are commonly of interest to ecologists. Access to food resources and predation are common causes of limitation. Effects relating to food and predation are often examined separately, but there is a great deal of evidence from theoretical and field studies that these factors interact and should be considered simultaneously (Abrams 1983, McNamara and Houston 1987, Krebs et al. 1995, Hubbs and Boonstra 1997, 1998). Access to food resources is important for reproduction and to avoid starvation, but foraging behaviors often increase predation risk. Individuals should seek a balance that minimizes predation risk while maximizing food intake. Such trade-offs have obvious implications for survival and abundance and may impact other vital rates, such as reproduction as well (Lima and Dill 1989). Studies seeking to understand dynamics of prey species will be benefited by investigating the roles of food resources and predation individually and in combination on multiple vital rates.

For the target species in this study, cotton and oldfield mice (*Peromyscus gossypinus* and *P. polionotus* respectively), a third factor may interact with food and predation: prescribed fire. Prescribed fire is a common management tool in longleaf pine, southern pine, and Florida scrub ecosystems in which both species occur (Whitaker and Hamilton 1998). Over the short term, burning simultaneously consumes food resources and reduces cover which increases exposure to predators. Over the long term, burning maintains open habitat, reduces occurrence of hardwood trees and shrubs, and improves vegetative growth (Brockway and Lewis 1997). Prescribed fire

benefits these species over the long term, although the exact form of the response may depend on frequency of fire application (Masters et al. 2002, 2007, Suazo et al. 2009). Most previous studies examining fire effects on small mammals focused on short term (less than one year) effects on abundance. These have shown cotton mice to respond to fire either neutrally or with immediate but temporary population spikes in burned areas (Shadowen 1963, Hatchell 1964, Layne 1974, Suazo et al. 2009). Oldfield mice do not appear to have a strong short-term fire response (Arata 1959, Odum et al. 1973, Suazo et al. 2009). We know of no studies that have attempted to experimentally determine which fire-related changes (loss of food resources or loss of cover) are responsible for the observed population-level effects, and few that have examined effects on a broader range of population parameters such as survival and reproduction.

The objective of this study was to experimentally examine the effects of supplemental feeding and mammalian predation on cotton and oldfield mouse populations. We were secondarily interested in determining the roles of these factors in changes in cover and food availability caused by prescribed burning. This was accomplished by establishing a large scale factorial experiment with mammalian predator exclusion and supplemental feeding treatments conducted over four and half years. Plots were burned three times over the course of the experiment.

Methods

Study Site and Species

This research was conducted at the Joseph W. Jones Ecological Research Center at Ichauway in Baker County, Georgia. Ichauway is a 12,000 ha property consisting primarily of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) ecosystem. Longleaf pine ecosystems are characterized by a low-density longleaf pine

over-story, a diverse, herbaceous groundcover, and an open, park-like mid-story (Van Lear et al. 2005). Hardwood tree species occur at limited levels. Frequent, low intensity fires are key ecological processes. Consequently, frequent application of prescribed fire is a primary management tool throughout Ichaaway; most sites are burned on a two year rotation (Atkinson et al. 1996).

Cotton and oldfield mice are common across the Southeastern US. The semi-arboreal cotton mouse prefers bottomland hardwood forests, but the species is a habitat generalist (Whitaker and Hamilton 1998). Downed woody debris is an important microhabitat component for this species (McCay 2000). Oldfield mice prefer dry, open fields with loose soils and beaches. This species is noted for its monogamous breeding habits (Whitaker and Hamilton 1998).

Field Methods

In 2002, the Jones Center constructed four mammalian predator exclosures, each paired with a nearby control with similar habitat. Plots range in size from 35.94 to 49.09 ha. Exclosures are surrounded by 1.2 m tall woven wire fences which carry electrified lines along the top, middle, and bottom to discourage mammals from climbing over or digging under (the weave is large enough to allow small mammals and snakes to pass through). Although mammalian predators occasionally enter exclosures, regular monitoring by track counts and thermal camera surveys indicate significantly fewer mammalian predators in exclosures than controls (Conner et al. 2010).

Each control and exclosure contained a 12x12 small mammal trapping grid with 15 m spacing between stations. Twenty-four elevated trapping stations were also interspersed throughout each grid, attached to trees at heights of about 1.5 to 2 m. Pairs of grids were trapped four times per year (once each season) from January 2005

through June 2007 and eight times per year (twice per season) from July 2007 through the June 2009 using Sherman live traps (H.B. Sherman Traps, Tallahassee, Florida, USA). A small amount of a granular insecticide was sprinkled around each trap to prevent deaths due to fire ants. New captures were marked individually with metal ear tags. Data recorded for all captures included location, species, sex, weight, age (adult or juvenile, based on weight), reproductive condition (for males, testes descended or not, for females, if pregnant and/or lactating), and hind foot measurement.

In June of 2007, two enclosure and two control grids were randomly selected to receive a supplemental feeding treatment consisting of placing 113 g (4 oz) of commercial rabbit chow in cans at every other station on the trapping grids. Food was replaced every other week. Empty cans were also placed in the non-feeding grids. This treatment continued through August 2009. Images from trail cameras demonstrated that cotton mice, oldfield mice, cotton rats (*Sigmodon hispidus*), house mice (*Mus musculus*), woodrats (*Neotoma floridana*), flying squirrels (*Glaucomys volans*), and eastern cottontails (*Sylvilagus floridanus*) regularly used feeding stations. We found no evidence that cans were defended by individuals of any species.

In February of 2005, 2007, and 2009, all plots were burned according to Ichauway's burn plan which has these study areas on a two year burn rotation. Trapping methods followed recommendations of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Florida Institutional Animal Care and Use Committee.

Statistical Methods

Data considered for this analysis includes capture-mark-recapture (CMR) data for cotton and oldfield mice trapped between January 2005 and June 2009 (26 sessions).

Analyses were carried out using the R 2.9.1 (R Development Core Team) package RMark (Laake and Rexstad 2008) to build models for program MARK (White and Burnham 1999).

Multistate CMR models were used to estimate and model state specific survival (S), capture probability (p), and transitions between reproductive states (Ψ). States used for S and Ψ were based on reproductive condition. Males were considered to be in reproductive condition if testes were descended, females if pregnant and/or lactating. Therefore, models evaluating effects on S which include a reproductive condition term estimate and model survival separately for reproductive and non-reproductive individuals, and models evaluating effects on Ψ which include a reproductive condition term estimate and model probabilities of individuals moving between reproductive states (i.e., rates of non-reproductive individuals entering reproductive states, rates of reproductive individuals remaining reproductive).

Preliminary analyses considered the potential influence of session, season, and year on p . Influence of reproductive condition and sex was assessed for S and Ψ . Breeding season was also considered for Ψ . Assessment of effects on p , S and Ψ was carried out in a sequential fashion. First, effects on p were considered while modeling S and Ψ using the most general models for each described above. Effects on S and Ψ were then considered in a similar fashion.

Assessment of goodness-of-fit was carried out using the median \hat{c} approach in program MARK (White and Burnham 1999). The median \hat{c} test indicated a mild overdispersion ($\hat{c} = 1.321$ for cotton mice and $\hat{c} = 1.339$ for oldfield mice). Models in each parameter's set were compared using Akaike's information criterion corrected for

small sample size (AICc), after quasi-likelihood adjustments (QAICc) made using $\hat{c} = 1.321$ for cotton mice and 1.339 for oldfield mice. Models were considered well supported if they had a ΔQAICc of less than two. The best supported model within each parameter's set was selected a base for modeling that parameter in further analyses.

These analyses indicated that reproductive condition and sex, modeled in an additive fashion, were important factors for describing S in cotton mice ($S(\text{reproductive condition}+\text{sex})$, Table 3-3 model 5), while reproductive condition was important for oldfield mice ($S(\text{reproductive condition})$, Table 3-4, model 5). For both species, capture probability was best described as fully time varying ($p(\text{session})$), Table 3-3, model 1 (cotton mice); Table 3-4, model 1 (oldfield mice)).

To model Ψ , we investigated approach to modeling a breeding season effect on Ψ . Breeding seasons vary over the geographic range of cotton and oldfield mice (Wolfe and Linzey 1977, Whitaker and Hamilton 1998). Throughout most of the range, breeding may occur year round but with peaks at certain times of the year. Because a literature review did not give a clear indication of when peak breeding seasons for these species occur in southwestern Georgia, we created model set, based on the literature (Wolfe and Lindzey 1977, Whitaker and Hamilton 1998, Suazo et al. 2009) and personal observations, to identify when peak breeding seasons occurred. This analysis indicated, for cotton mice, breeding peaks in fall and early winter (Table 3-1, model 1), and, for oldfield mice, peaks in winter and summer (Table 3-2, model 1).

Because of potential confounding effects due to prescribed burning treatments and breeding seasons occurring as occasion-dependant effects, we then assessed whether

there was evidence to support further division of cotton mouse non-breeding seasons into whether a burn occurred during these seasons or not. Since the burns occurred during the oldfield mouse peak breeding season, a similar division was made, but with respect to peak breeding seasons rather than non-peak seasons. Further division of breeding seasons based on burning was well supported (Table 3-1, model 7 for cotton mice, and Table 3-2, model 5 for oldfield mice).

Using these breeding season models, we continued the sequential variable selection for Ψ as described above for p and S . Reproductive condition, sex, and breeding season, modeled in an additive fashion, were important for modeling Ψ in cotton mice ($\Psi(\text{reproductive condition}+\text{sex}+\text{breeding seasons})$, Table 3-3, model 10), while reproductive condition and breeding season, also modeled in an additive fashion, were important for oldfield mice ($\Psi(\text{reproductive condition}+\text{breeding season})$, Table 3-4, model 10).

Although the prescribed fires occurred at specific times, fire-caused changes in cover and food resources may last for weeks or months. To determine the best effect window for the fire treatments, a set of models considering fire effects on survival over multiple time intervals was considered. Survival was constrained to be similar between all trapping periods except those following fires. Post-fire survival was allowed to vary for several different intervals, from including only the interval during which the fire occurred (interval length of ten weeks following the 2005 and 2007 fires and of five weeks following the 2009 fire), to including intervals through the summer season (30 weeks), by which time vegetation is typically recovered. For both species no single model had overwhelming support over the others (Table 3-5). The top ranked model

was chosen to represent the fire effect on survival in subsequent analysis. For cotton mice, the highest ranking model indicated a short term fire effect on survival with declines occurring over a period of ten weeks (Table 3-5, model 1). For oldfield mice, the best supported model indicated an effect lasting thirty weeks (Table 3-5, model 5).

Exclosure and control sites were initially selected as pairs based on similar habitats between pairs. As part of a post-hoc examination of non-treatment effects on S and Ψ , we examined the potential for paired site effects on these parameters. Using the best models indicated by the analyses described above, we ran a second set of models considering paired site effects on S and Ψ . This analysis indicated paired site effects were important in modeling both S and Ψ for cotton and oldfield mice (Table 3-6, model 1 (cotton mice) and model 5 (oldfield mice)).

Treatment effects were added to the best base model (for cotton mice: $S(\text{reproductive condition}+\text{sex}+\text{site})\rho(\text{session})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site})$; for oldfield mice: $S(\text{reproductive condition}+\text{site})\rho(\text{session})\Psi(\text{breeding season}+\text{reproductive condition}+\text{site})$) as additive and interactive effects (two-way only). Due to confounding effects relating to both fire and breeding season occurring as occasion-dependant effects, only supplemental feeding and predation treatments were considered with respect to Ψ , while feeding, predation, and fire effects were considered with respect to S . Model averaging was employed to generate parameter estimates for S and Ψ .

Abundance estimates (N) were also generated for both species. Pollock's robust design (Pollock 1982) was used for cotton mice. Due to computational difficulties, it

was not possible to use the robust design for oldfield mice; the POPAN model was used instead (Schwarz and Arnason 1996).

Robust design models estimate probabilities for survival (S), capture (p), recapture (c), emigration (γ''), and staying away after emigration (γ'). The variable selection approach used for the robust design was similar to that used for the multistate analysis. Preliminary investigation considered potential for time and sex effects on p and c . Paired site effects were considered for N . S was modeled using the best S model from the multistate analysis (without reproductive condition; $S(\text{sex}+\text{site}+\text{fire}*\text{predation})$). γ terms were modeled using a random emigration effect ($\gamma''(\cdot)=\gamma'(\cdot)$).

Preliminary investigations indicated that cotton mouse capture/recapture models were best supported when modeled with a capture probability that varied by session and allowed a constant “trap happy” response. Sex was also important for modeling capture/recapture probabilities ($p(\text{session}+\text{sex})c(p+c')$ where c' is the constant trap happy response, Table 3-7, model 3). Paired site effects were important for N (Table 3-7, model 1).

Because of the difficulties associated with modeling treatment effects on abundance directly (White 2002), the best robust design model indicated by the preliminary analysis described above, $S(\text{sex}+\text{site}+\text{fire}*\text{predation})\gamma''(\cdot)=\gamma'(\cdot)$ $p(\text{session}+\text{sex})c(p+c')N(\text{site})$, was used to generate derived abundance estimates by site and session, but not to assess treatment effects. Treatment effects on abundance were evaluated using a repeated measures ANOVA (Schabenberger and Pierce 2002) implemented using the PROC MIXED procedure in SAS (SAS Institute Inc. 2004). The variables considered in this ANOVA included food, fire, and predation treatments and

their interactions (two-way interactions only). Paired sites were included as a random effect. Multiple covariance structures were investigated and the best (variance components structure, which allows a different variance for each random effect) was selected based on AICc value (Miller et al. 2004). Treatment effects were considered significant at the $\alpha = 0.05$ level.

The POPAN models used for oldfield mice estimate apparent survival (Φ), capture probability (p), entry probability ($pent$), and population size (N). Due to constraints associated with the POPAN model, the data set was divided by paired sites. For each of these paired sites, Φ was modeled using the best survival model from the multistate analysis (minus the reproductive condition term; $\Phi(\text{predation})$). The sequential variable selection process for N , p , and $pent$ followed as described previously. A site effect was considered with respect to N . Effects of year, burn year, and season were considered with respect to p and $pent$. To pick the best common model for all site pairs, each candidate model in each parameter's candidate model set was ranked by ΔAICc score. Ranks were summed across sites for each parameter and the model with the lowest score was selected as the best. This investigation determined that p and $pent$ were best modeled across sites using an additive effect between year and season while N was best modeled varying by site (Table 3-8).

The resulting model $\Phi(\text{predation})p(\text{year}+\text{season})pent(\text{year}+\text{season})N(\text{site})$ was run for all site pairs to generate derived abundance estimates for each site by trapping session. Treatment effects on abundance were investigated using a repeated measures ANOVA in PROC MIXED in SAS as described above for cotton mice.

Results

Cotton Mice

A total of 2108 individual cotton mice (8428 total captures) was trapped over 26 trapping sessions in eight trapping plots. The best supported multistate model suggested an interactive effect of predation and fire treatments on survival with an interactive effect of feeding and predation on Ψ (Table 3-9, model 1). Although this model was the best supported (the second ranked model has a $\Delta QAI Cc > 2$), it did not carry a great deal of weight (0.393). However, it was clear from the top ranked models that the feeding interacted with predation to affect Ψ . This interaction appeared in the top ten models, and models with this interaction held 91.1% of the weight of the overall model set. Support for treatment effects on survival was less clear. The second best supported model (model 2, Table 3-9) included no treatment effect on survival, indicating poor support for treatment effects other than the interactive predation*fire effect on survival.

The lack of substantial support for any particular model indicates model selection uncertainty; therefore, model averaging was employed for parameter estimation. Overall model averaged survival estimates showed that males had lower survival than females and that reproductive individuals had higher survival than non-reproductive individuals (Figure 3-1). Model averaged estimates indicated that, in predator access grids, burning had essentially no effect on survival. In predator exclosures, however, survival increased dramatically following fires (Figure 3-1). During non-fire periods, survival was slightly greater in predator access grids than in the exclosures, but this trend was reversed following burns (Figure 3-1).

The addition of food had minimal impact on survival regardless of whether predators had access or not, or whether an area had been recently burned or not (Figure 3-1).

Model averaged parameter estimates for Ψ showed that a greater proportion of males made transitions to reproductive states than females in all seasons (Figure 3-2). Additionally, most reproductive individuals that achieved a reproductive state stayed in a reproductive state; this trend was slightly greater for males than females (Figure 3-2).

Initial investigation indicated a strong fire effect on transitions between reproductive states: models that included three classes of breeding seasons (peak breeding in fall and early winter, non-peak breeding in springs, summers, and late winters without burns, and a second non-peak in springs, summers, and late winters of burn years; hereafter, peak, non-peak/non-burn, and non-peak/burn respectively) had greater support than models with only two breeding seasons (peak and non-peak with no distinguishing between burn and non-burn years). Two-season models had no support (weight = 0.0) compared to three-season models (Table 3-1, model 7).

Model averaged parameter estimates indicated that transitions to reproductive states were at their highest during peak breeding seasons and that there was a small drop in transitions to reproductive states during non-peak/non-fire seasons (Figure 3-2). Transitions to reproductive states dropped considerably more during non-breeding/fire seasons (Figure 3-2). Predator exclusion and feeding alone caused small decreases in reproductive transitions and the combination of these treatments was associated with an increase in transitions to reproductive states (Figure 3-2).

The repeated measures ANOVA examining treatment effects on abundance indicated a significant effect of feeding on abundance ($P < 0.001$). Examination of least square means indicated that feeding plots contained 1.8x the number of cotton mice as unfed plots. No other treatments or their interactions significantly affected abundance ($P > 0.05$).

Oldfield Mice

A total of 1203 individual oldfield mice (4828 total captures) was trapped over 26 trapping sessions in eight trapping plots. There was no clear top multistate model for oldfield mice as there were six models with a $\Delta\text{QAICc} < 2$ and none of these carried much weight (Table 3-10). However, it was clear from the top ranked models that predation was an important factor affecting survival. Predation effects appeared in the top twenty models and these models collectively held a weight of 82.8%. Models including feeding also had decent support in the model set, holding 67% of the weight of the overall set. The model set showed limited support for treatment effects on Ψ . The lack of clear support for any particular model indicated model selection uncertainty; therefore, model averaging was employed for parameter estimation.

Model averaged survival estimates indicated that non-reproductive individuals had lower survival than reproductive individuals (Figure 3-3). Model averaged survival estimates also showed increased survival in predator exclusion plots compared to predator access plots. This was true in both pre- and post-fire periods. Following prescribed fires, survival decreased slightly in predator access grids and increased (by a slightly greater magnitude) in predator exclosure treatments (Figure 3-3). Addition of food was associated with declines in survival in both predator access and exclosure grids, and in both pre- and post-fire periods. The magnitude of the decline was greater

in enclosures than in controls, but the magnitude of the change was not great in either case.

Initial investigation found strong fire effects on transitions between reproductive states: models that included three classes of breeding seasons (bimodal peak breeding in winters and summers, distinguishing between burn years and non-burn years, and non-peak breeding in falls and springs) had better support than models that contained only two breeding seasons (peak and non peak, with no distinguishing between burn and non-burn peak seasons). Two season models had no support when compared to three season models (weight = 0.0, Table 3-2, model 5).

Model averaged parameter estimates for Ψ indicate that a greater proportion of reproductive individuals that achieved reproductive states stayed in reproductive states (Figure 3-4). Transitions to reproductive states were the greatest during peak breeding seasons of non-burn years. Transitions into breeding states dropped during non-peak seasons. However, during winters and summers of burn years, transitions to breeding states dropped dramatically such that transitions during these seasons were below even that of non-breeding seasons, indicating a strong fire effect on reproduction in oldfield mice (Figure 3-4).

Predator exclusion was associated with smaller proportions of individuals entering breeding states, whether food was present or not, although this difference was minimal. Supplemental feeding was associated with a larger increase in transitions to reproductive states in both predator access and exclusion areas (Figure 3-4).

The repeated measures ANOVA examining treatment effects on abundance indicated significant effects of predation and feeding treatments and the interaction of

these treatments on abundance ($P = 0.001$, $P < 0.001$, and $P = 0.001$ respectively). Examination of least square means showed that feeding increased abundances by 2.7x, predator exclusion increased abundances by 2.7x and the application of both treatments simultaneously increased abundances by 7.6x.

Discussion

Although cotton and oldfield mice are closely related species which occur in many of the same habitats, they were affected in different ways by the application of mammalian predator exclusion, supplemental feeding, and prescribed fire treatments. However, both species showed a surprising trend of increased survival among reproductive individuals compared to non-reproductive individuals. We hypothesize that this may be because non-reproductive adults are likely to be younger individuals. Although there is evidence that reproduction exacts a survival cost among small mammals (Koivula et al. 2003), it may be that among these mice, the cost of being young is greater. Juveniles and young adults tend to be transient while seeking to establish home ranges (Bigler and Jenkins 1975) and dispersal behavior is associated with reduced survival (Van Vuren and Armitage 1994). However, this behavior may be adaptive in general if dispersed individuals improve reproduction by doing so (Van Vuren and Armitage 1994).

Among cotton mice, initial analyses identified sex as an important factor with respect to both survival and reproductive transitions, but among oldfield mice sex was irrelevant. It is possible that this difference occurs because oldfield mice are monogamous and form long-term pair bonds while cotton mice are promiscuous (Blair 1951).

Treatment Effects on Cotton Mice

Cotton mice showed different treatment effects on different vital rates, some in interactive and unexpected ways. It is difficult to tie these effects into a clear picture of how predation, food resources, and fire affect cotton mouse populations overall, but interpretation is aided by consideration of ecological theory concerning adaptive prey behavior in response to predation risk and food availability. This theory has been largely developed by Abrams (1983, 1984, 1991, 1992a, 1992b, 1993) and is based on the observation that while access to sufficient food is required for reproduction and to avoid starvation, foraging increases predation risk. Individuals must make trade-offs between foraging and predation risk in such a way as to maximize food intake (and by extension, reproduction) while minimizing mortality. A large body of theoretical and experimental evidence suggests such trade-offs are common (reviewed in Lima and Dill 1989) and may be stronger than direct consumptive effects of predation (Pressier et al. 2005). Although a simple concept at the core, the effects of these adaptive behaviors may be complex and counterintuitive (Abrams 1991, 1992a, 1992b, 1993). This is especially likely in systems with complex food webs and competitive interactions between multiple predator and prey species. Effects of trade-offs may also depend on a species' life history and may change with breeding/non-breeding seasons (Abrams 1991).

The only strong treatment effect on cotton mouse survival was an increase in survival with the combination of predator exclusion and fire. There was no strong fire effect on survival in predator controls, and survival was similar between controls and exclosures during non-fire periods. This suggests fire conveys a benefit that is not realized when predators have access to the burned area. This in turn suggests an

awareness of increased predation risk with loss of cover, a behavioral response of cotton mice in the predator controls, and a choice to balance predation risk against taking advantage of this benefit. Differences in predation and associated trade-offs may contribute to the mixed short-term fire responses (neutral or beneficial) observed with cotton mice in previous studies (Shadowen 1963, Hatchell 1964, Layne 1974, Suazo et al. 2009).

The general lack of a supplemental feeding effect on survival suggests that food resources are not important in this fire response, unless the food supplementation was insufficient or access to food cans was considered risky. Other mechanisms that may have caused to the combined benefit of fire and predator exclusion remain unclear. It is possible that change in abundances of other species in the burned area may have contributed to this response. For example, cotton rats, usually among the most abundant species in the study areas, declined to near 0 following burns.

The combination of a lack of a fire effect on abundance and a decline in post-fire breeding supports a behavioral response to increased predation risk associated with post-fire conditions. Adaptive anti-predatory behavior may mitigate negative fire effects on survival and abundance, but a trade-off appears to occur with a decline in reproduction. Because fires occurred during the non-breeding season, it is reasonable that cotton mice would make a trade off favoring survival at the cost of reproduction. Population growth rates of species such as rodents which mature rapidly and reproduce often are most sensitive to changes in reproduction (Heppell et al. 2000, Oli and Dobson 2003), and in most cases ought to favor strategies that maximize reproduction rather than survival. However, during the non-breeding season these species should

maximize fitness by behaving in a similar manner as semelparous species (Abrams 1991). This entails minimizing predation risk by reducing foraging. That feeding had no apparent effect on post-fire survival and reproductive transitions may be explained by the observation that for semelparous species, or iteroparous species in the non-breeding season, increases in food resources should, somewhat counterintuitively, be associated with a decrease in foraging effort to maximize survival and overall fitness (Abrams 1991).

Increased predation should cause prey species to make trade-offs between growth rate (positively associated with food intake) and predation risk (negatively associated with food intake) when prey species (like cotton mice) achieve reproductive maturity at a specific size rather than by reaching a specific age (Abrams and Rowe 1996). This trade-off should cause an increase in predation risk to be associated with an increase in the age at maturity due to decreased growth rates (Abrams and Rowe 1996). This relationship may have contributed to the decline in reproduction following fires; if juvenile development was delayed, a decline in reproductive transitions should be observed. However, increases in food resources may counteract the direct effect of predation on growth rate (Abrams and Rowe 1996). This may explain why breeding transitions were positively affected by the interaction of predator exclusion and food supplementation.

Food addition was associated with a nearly two-fold increase in abundance. It is not surprising that food addition caused increases in abundance, but given the relationship between food resources and the ability to achieve reproductive status in small mammals (Cameron and Eshelman 1996), it is interesting that feeding was not

also associated with increases in transitions to reproductive states (except in predator exclusion plots). This suggests that the increased abundances were due to either increases in juvenile survival, in the number of young produced per reproductive event or immigration to feeding plots. Such effects have been observed to occur in response to supplemental feeding in previous studies with small mammals (Boutin 1990, Hubbs and Boonstra 1997); unfortunately, we were unable to address these factors in the current study.

Treatment Effects on Oldfield Mice

The strongest treatment effect on oldfield mice was the predator exclusion treatment; this was associated with increased survival and abundance. Feeding and the interaction of feeding and predator exclusion were also associated with increased abundances. On the surface, these results seem more intuitive than the cotton mouse results and could be interpreted to suggest oldfield mice are more influenced by direct consumptive effects of predation. Pressier and Bolnick (2008) observed in a review of non-consumptive effects of predation that non-consumptive effects seemed to dominate some predator-prey relationships while appearing to be weak or non-existent in others. However, Peckarsky et al. (2008) note that it is impossible to conclude that changes in prey survival and abundance are due solely to direct effects of predation as stresses and trade-offs associated with predation risk can cause declines in survival and abundance even when prey are not actually at risk (as by experimental manipulation of a predator's ability to kill). Such indirect effects may be overlooked when they take the predicted form and direction of direct consumptive effects, and they may at times cause effects as strong, if not stronger, than direct consumptive effects (Pressier et al. 2005). Behavioral data can help to distinguish between direct and indirect effects, and indeed

may be necessary to do so (Abrams 1995), but our study design did not include such observations.

Similar to the results observed with cotton mice, feeding was associated with increases in abundance but with only minimal increases in reproductive transitions, indicating the feeding effect on abundance may be due to increases in immigration, juvenile survival, or the number of young produced per reproductive event.

Predation had a minimal effect on reproductive transitions, but fire caused declines in transitions to reproductive states. Given the importance of predation on other population parameters, it might be expected that there would be an interaction of predation and fire treatments since burning removes cover and should increase risk of predation. It is possible that increased predation due to loss of cover was not a problem following fires because this species already prefers open areas (Whitaker and Hamilton 1998). This of course fails to explain why burning caused declines in reproductive transitions, and why addition of food was insufficient to prevent such declines. Although the decline in reproductive transitions following fires is similar to that of cotton mice, an important difference exists between the responses in these species. Cotton mice were in a non-peak breeding season when the burns occurred while oldfield mice were in a peak season. In this situation, oldfield mice should be expected to maximize reproduction during this season, even at the expense of survival (Abrams 1991). That they were unable to do so (assuming reproductive output is associated with transitioning to a reproductive state) suggests that either the theory is incorrect or that oldfield mice were limited in some way despite food addition. Given necessity of sufficient food quality and quantity for small mammals to achieve reproductive status (Cameron and

Eshelman 1996), and the oldfield mouse's general dietary preference for insects and seeds over herbaceous material, it is possible that the provided food was insufficient to allow these mice to maintain normal breeding following a winter burn. Although supplemental food was available following fires, other preferred food sources may have become limiting. For example, Odum et al. (1973) observed declines in arthropod abundances following a winter burn in Georgia for several months.

Conclusions

Although cotton and oldfield mice are closely related species that occur in similar habitats, feeding, fire, and predation treatments affected these species differently. Cotton mice appear to make trade-offs with respect to predation risk. These appear to be especially important following fire events, implying cotton mice are, over the short term, negatively affected by the loss of cover associated with burning. An exception seems to occur when mammalian predators are excluded. Oldfield mice also experience significant effects of predation but it is less clear if these effects are related directly or indirectly to consumption itself, or merely the risk of being consumed. Fire effects are less apparent for oldfield mice although reproduction in oldfield mice is negatively affected by fires.

The retroductive conclusions relating to behavioral responses are in many ways speculative as we lack behavioral data that would help to confirm these effects. Studies incorporating behavioral components such as home range size, microhabitat use, giving up densities for foraging animals, etc., could better address these issues.

Table 3-1. Model comparison table for multistate capture-mark-recapture analysis assessing occurrence of peak breeding seasons of cotton mice in general (Model set 1) and with respect to winter prescribed burns (Model set 2) in Southwestern Georgia between 2005 and 2009. All models had survival set as S(reproductive condition+sex) and capture probability set as p(session). Table includes number of parameters (K), model weights (relative likelihood of models in the set), and difference in Akaike's information criterion corrected for small sample size after quasiliikelihood adjustment ($\Delta QAI Cc$). Quasiliikelihood adjustments were made using an estimated \hat{c} of 1.339.

	Model no.	Model	K	$\Delta QAI Cc$	Model weight
Model set 1*	1	Ψ (fall and early winter peaks)	30	0.00	1.00
	2	Ψ (winter, spring and fall peaks)	30	24.82	0.00
	3	Ψ (fall peaks)	30	32.17	0.00
	4	Ψ (winter peaks)	30	64.67	0.00
	5	Ψ (fall and winter peaks)	30	72.68	0.00
	6	Ψ (constant)	29	75.55	0.00
Model set 2**	7	Ψ (fall and early winter peaks; late winter, spring, summer non-peaks divided by burn years and non-burn years)	31	0.00	1.00
	8	Ψ (fall and early winter peaks; late winter, spring, summer non-peaks)	30	18.70	0.00

* Model set 1 considers only two classes of breeding season: peak (listed) and non-peak (all seasons not listed for a given model).

** Model set 2 compares the best model from set 1 (model number 1) with a similar model that considers three classes of breeding seasons by breaking down non-peak seasons into those that occurred during burn years (late winters, springs, and summers of 2005, 2007, and 2009; burns occurred in mid-winters of these years) and those that occurred during non-burn years (late winters, springs, and summers of 2006 and 2008).

Table 3-2. Model comparison table for multistate capture-mark-recapture analysis assessing occurrence of peak breeding seasons of oldfield mice in general (Model set 1) and with respect to winter prescribed burns (Model set 2) in Southwestern Georgia between 2005 and 2009. All models had survival set as S (reproductive condition) and capture probability set as p (session). See Table 3-1 for column definitions.

	Model no.	Model	K	$\Delta QAICc$	Model weight
Model set 1*	1	Ψ (winter and summer winter peaks)	29	0.00	0.59
	2	Ψ (spring peaks)	29	2.56	0.16
	3	Ψ (no peaks)	28	2.73	0.15
	4	Ψ (fall peaks)	29	3.49	0.10
Model set 2**	5	Ψ (winter and summer peaks with peak seasons divided by burn years and non-burn years)	30	0.00	1.00
	6	Ψ (winter and summer peaks)	29	41.07	0.00

* Model set 1 considers only two classes of breeding season: peak (listed) and non-peak (all seasons not listed for a given model).

** Model set 2 compares the best model from set 1 (model number 1) with a similar model that considers three classes of breeding seasons by breaking down the peak seasons into those that occurred during burn years (winters and summers of 2005, 2007, and 2009; burns occurred in winters of these years) and those that occurred during non-burn years (winters and summers of 2006 and 2008).

Table 3-3. Model comparison table for multistate capture-mark-recapture analysis assessing sex, reproductive condition, breeding season, and time effects on capture probability (p), survival (S), and transitions rates between reproductive states (Ψ) in cotton mice in Southwestern Georgia between 2005 and 2009. See Table 3-1 for column definitions.

Model no.		K	$\Delta QAI C_c$	Model weight
Effects on capture probability (p) *				
1	$p(\text{session})$	34	0.00	0.71
2	$p(\text{season})$	14	1.84	0.29
3	$p(\text{constant})$	10	12.84	0.00
4	$p(\text{years})$	14	13.65	0.00
Effects on survival (S)**				
5	$S(\text{reproductive condition}*\text{sex})$	34	0.00	0.48
6	$S(\text{reproductive condition}+\text{sex})$	33	0.47	0.38
7	$S(\text{sex})$	32	3.83	0.07
8	$S(\text{reproductive condition})$	32	4.14	0.06
9	$S(\text{constant})$	31	6.44	0.02
Effects on rates of reproductive transitions***				
10	$\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	33	0.00	0.61
11	$\Psi(\text{breeding season}+\text{reproductive condition})$	32	0.93	0.39
12	$\Psi(\text{breeding season}+\text{sex})$	32	245.32	0.00
13	$\Psi(\text{breeding season})$	31	254.10	0.00
14	$\Psi(\text{constant})$	29	348.35	0.00

Additional parameters modeled as $S(\text{reproductive condition}\text{sex})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

**Additional parameters modeled as $p(\text{session})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

***Additional parameters modeled as $S(\text{reproductive condition}*\text{sex})p(\text{session})$.

Table 3-4. Model comparison table for multistate capture-mark-recapture analysis assessing sex, reproductive condition, breeding season, and time effects on capture probability (p), survival (S), and transitions rates between reproductive states (Ψ) in oldfield mice in Southwestern Georgia between 2005 and 2009. See Table 3-1 for column definitions.

Model no.	Model	K	$\Delta QAI Cc$	Model weight
Effects on capture probability (p) *				
1	$p(\text{session})$	34	0.00	0.84
2	$p(\text{season})$	14	3.31	0.16
3	$p(\text{years})$	14	22.05	0.00
4	$p(\text{constant})$	10	23.60	0.00
Effects on survival (S)**				
5	$S(\text{reproductive condition})$	32	0.00	0.43
6	$S(\text{reproductive condition}+\text{sex})$	33	0.18	0.40
7	$S(\text{reproductive condition}*\text{sex})$	34	1.98	0.16
8	$S(\text{sex})$	32	8.32	0.01
9	$S(\text{constant})$	31	8.55	0.01
Effects on rates of reproductive transitions (Ψ)***				
10	$\Psi(\text{breeding season}+\text{reproductive condition})$	33	0.00	0.54
11	$\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	34	0.36	0.46
12	$\Psi(\text{breeding season}+\text{sex})$	33	51.21	0.00
13	$\Psi(\text{breeding season})$	32	51.34	0.00
14	$\Psi(\text{constant})$	30	93.94	0.00

Additional parameters modeled as $S(\text{reproductive condition}\text{sex})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

**Additional parameters modeled as $p(\text{session})\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$.

***Additional parameters modeled as $S(\text{reproductive condition}*\text{sex})p(\text{session})$.

Table 3-5. Model comparison table for multistate capture-mark-recapture analysis assessing term of effect of winter prescribed burns on survival of cotton and oldfield mice in Southwestern Georgia between 2005 and 2009. See Table 3-1 for column definitions. All models had additional parameters of capture probability (p) modeled as $p(\text{session})$ and rate of transition between reproductive states (Ψ) modeled as $\Psi(\text{reproductive condition}+\text{sex}+\text{breeding season})$ (for cotton mice) or $\Psi(\text{reproductive condition}+\text{breeding season})$ (for oldfield mice).

Species	Model no.	Model	K	ΔQAICc	Model weight
Cotton mice	1	S(fire effect over 10 weeks)	32	0.00	0.32
	2	S(fire effect over 20 weeks)	32	0.35	0.27
	3	S(fire effect over 5 (2009) to 10 weeks (2005 and 2007))*	32	0.81	0.21
	4	S(fire effect over 30 weeks)	32	0.85	0.21
Oldfield mice	5	S(fire effect over 20 weeks)	32	0.00	0.28
	6	S(fire effect over 30 weeks)	32	0.25	0.24
	7	S(fire effect over 10 weeks)	32	0.26	0.24
	8	S(fire effect over 5 (2009) to 10 weeks (2005 and 2007))*	32	0.31	0.24

* Models 3 and 8 show a range of intervals because the interval between trapping sessions changed from 10 weeks (2005 and 2007) to 5 weeks (2009) before the 2009 prescribed burn.

Table 3-6. Model comparison table for multistate capture-mark-recapture analysis assessing potential for site effects on survival (S) and rate of transitions to reproductive states (Ψ) of cotton and oldfield mice in Southwestern Georgia between 2005 and 2009. See Table 3-1 for column definitions. All models had capture probability (p) modeled as $p(\text{session})$.

Model no.	Species	Model	K	ΔQAICc	Model weight
1	Cotton Mice	$S(\text{reproductive condition}+\text{sex}+\text{site}^*)$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site})$	39	0.00	0.68
2		$S(\text{reproductive condition}+\text{sex}+\text{site})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	36	1.49	0.32
3		$S(\text{reproductive condition}+\text{sex})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex}+\text{site})$	36	19.99	0.00
4		$S(\text{reproductive condition}+\text{sex})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{sex})$	33	21.63	0.00
5	Oldfield Mice	$S(\text{reproductive condition}+\text{site})$ $\Psi(\text{breeding season}+\text{reproductive condition}+\text{site})$	38	0.00	0.68
6		$S(\text{reproductive condition})\Psi(\text{breeding season}+\text{reproductive condition}+\text{site})$	35	1.53	0.32
7		$S(\text{reproductive condition}+\text{site})\Psi(\text{breeding season}+\text{reproductive condition})$	35	16.43	0.00
8		$S(\text{reproductive condition})\Psi(\text{breeding season}+\text{reproductive condition})$	32	17.80	0.00

*Site effects are paired site effects. This effect pairs each site treated with mammalian predator exclusion with a predator access site with similar habitat.

Table 3-7. Model comparison table for robust design capture-mark-recapture analysis assessing demographic and time effects on abundance (N), capture probability (p), and recapture probability (c) in cotton mice in Southwestern Georgia between 2005 and 2009. See Table 3-1 for column definitions. Survival (S) was modeled as $S(\text{site}+\text{sex}+\text{fire}*\text{predation})$ for all models. Emigration terms (γ'' and γ') were modeled with a random emigration effect for all models: $\gamma''(\cdot)=\gamma'(\cdot)$.

Model no.	Model	K	ΔQAICc	Model weight
Effects on abundance (N)*				
1	$N(\text{site})$	41	0.00	1.00
2	$N(\cdot)$	38	21.69	0.00
Effects on capture (p) and recapture (c)**				
3	$p(\text{session}+\text{sex})c(p+c')^\dagger$	41	0.00	1.00
4	$p(\text{session})c(p+c')^{\dagger\dagger}$	40	29.03	0.00
5	$p(\text{sex})c(p+c')^\ddagger$	16	229.00	0.00
6	$p(\cdot)c(p+c')^{\ddagger\dagger}$	15	246.21	0.00
7	$p(\cdot)c(p)^\S$	14	362.08	0.00

* Additional parameters modeled as $p(\text{session}+\text{sex})c(p+c')$.

** Additional parameter modeled as $N(\text{site})$.

† Indicates capture probability varies by session, with an additive effect of sex, and with a constant trap happy response recapture response (c').

†† Indicates capture probability varies by session with a constant trap happy response recapture response (c').

‡ Indicates capture probability varies by sex with a constant trap happy response recapture response (c').

‡‡ Indicates a constant capture probability with a constant trap-happy recapture response (c').

§ Indicates constant capture and recapture rates (shared).

Table 3-8. Model comparison table for POPAN capture-mark-recapture analysis assessing site and time effects on abundance (N), capture probability (p), and entry probability (p_{ent}) in oldfield mice in Southwestern Georgia between 2005 and 2009. Effects are given separately for four paired mammalian predator exclusion and control sites. See Table 3-1 for column definitions. Survival (Φ) was modeled as $S(\text{predation})$ for all models. Bolded models indicate those selected as the best common model for all sites (based on ranking each model by ΔAICc score and summing ranks across sites).

Model no.	Model	K	ΔAICc	Model weight
Effects on abundance (N)*				
Control/Exclosure 1				
1	$N(\text{site})$	16	0.00	0.88
2	$N(\text{constant})$	15	4.08	0.12
Control/Exclosure 2				
3	$N(\text{site})$	16	0.00	1.00
4	$N(\text{constant})$	15	14.42	0.00
Control/Exclosure 3				
5	$N(\text{site})$	16	0.00	0.70
6	$N(\text{constant})$	15	1.71	0.30
Control/Exclosure 4				
7	$N(\text{constant})$	15	0.00	0.71
8	$N(\text{site})$	16	1.81	0.29
Effects on capture probability (p)**				
Control/Exclosure 1				
9	$p(\text{year}+\text{season})$	19	0.00	1.00
10	$p(\text{burn year}+\text{season})$	16	30.74	0.00
11	$p(\text{season})$	15	43.33	0.00
12	$p(\text{burn year})$	12	59.00	0.00
13	$p(\text{constant})$	11	60.36	0.00
14	$p(\text{year})$	15	60.39	0.00
Control/Exclosure 2				
15	$p(\text{year}+\text{season})$	19	0.00	0.99
16	$p(\text{year})$	15	9.29	0.01
17	$p(\text{season})$	15	116.85	0.00
18	$p(\text{burn year}+\text{season})$	16	118.94	0.00
19	$p(\text{constant})$	11	132.72	0.00
20	$p(\text{burn year})$	12	134.30	0.00
Control/Exclosure 3				
21	$p(\text{year}+\text{season})$	19	0.00	0.99
22	$p(\text{year})$	15	10.00	0.01
23	$p(\text{burn year}+\text{season})$	16	11.73	0.00
24	$p(\text{constant})$	11	11.93	0.00
25	$p(\text{burn year})$	12	14.11	0.00
26	$p(\text{season})$	15	18.09	0.00

Table 3-8. Continued

Model no.	Model	K	$\Delta AICc$	Model weight
Control/Exclosure 4				
27	$p(\text{year})$	15	0.00	0.37
28	$p(\text{burn year})$	12	0.13	0.35
29	$p(\text{constant})$	11	1.01	0.22
30	$p(\text{year+season})$	19	4.63	0.04
31	$p(\text{season})$	15	6.96	0.01
32	$p(\text{burn year+season})$	16	7.27	0.01
Effects on entry probability ($pent$)				
Control/Exclosure 1				
33	$pent(\text{year+season})$	19	0.00	0.93
34	$pent(\text{year})$	15	6.52	0.04
35	$pent(\text{burn year+season})$	16	6.86	0.03
36	$pent(\text{season})$	15	14.34	0.00
37	$pent(\text{burn year})$	12	20.30	0.00
38	$pent(\text{constant})$	11	28.42	0.00
Control/Exclosure 2				
39	$pent(\text{year+season})$	19	0.00	0.99
40	$pent(\text{year})$	15	9.93	0.01
41	$pent(\text{burn year+season})$	16	130.58	0.00
42	$pent(\text{burn year})$	12	136.50	0.00
43	$pent(\text{season})$	15	161.11	0.00
44	$pent(\text{constant})$	11	182.66	0.00
Control/Exclosure 3				
45	$pent(\text{season})$	15	0.00	0.60
46	$pent(\text{burn year+season})$	16	1.06	0.35
47	$pent(\text{constant})$	11	6.45	0.02
48	$pent(\text{burn year})$	12	7.57	0.01
49	$pent(\text{year+season})$	19	9.49	0.01
50	$pent(\text{year})$	15	15.81	0.00
Control/Exclosure 4				
51	$pent(\text{year+season})$	19	0.00	1.00
52	$pent(\text{burn year+season})$	16	21.86	0.00
53	$pent(\text{season})$	15	30.39	0.00
54	$pent(\text{year})$	15	106.40	0.00
55	$pent(\text{constant})$	11	138.22	0.00
56	$pent(\text{burn year})$	12	139.90	0.00

* Additional parameters modeled as $p(\text{burn year+season})$ and $pent(\text{burn year+season})$.

** Additional parameters modeled as $pent(\text{burn year+season})$ and $N(\text{site})$.

*** Additional parameters modeled as $N(\text{site})$ and $p(\text{burn year+season})$.

Table 3-9. Model comparison table for multistate capture-mark-recapture analysis examining the effect of predation, feeding, and fire treatments on survival (S) and transition probabilities (Ψ , between reproductive and non-reproductive states) of cotton mice in southwestern Georgia, 2005-2009. All models had capture probability set at $p(\text{session})$. See Table 3-1 for column definitions. Bolded text indicates treatment effects (all other effects are similar between models throughout the set). Table values were adjusted for an estimated \hat{c} of 1.321. Only models with a model weight > 0.03 are shown here (the top 8 models of 55 in the overall set).

Model no.	Model	K	ΔQAICc	Model weight
1	S(reproductive condition+sex+site+ predation*fire) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	45	0.00	0.39
2	S(reproductive condition +sex+site) $\Psi(\text{breeding season+ reproductive condition +sex+site+food*predation})$	42	2.08	0.14
3	S(reproductive condition +sex+site+ fire) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	43	2.73	0.10
4	S(reproductive condition +sex+site+ predation) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	43	3.81	0.06
5	S(reproductive condition +sex+site+ food) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	43	4.07	0.05
6	S(reproductive condition +sex+site+ food*fire) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	45	4.22	0.05
7	S(reproductive condition+sex+site+ predation+fire) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	44	4.39	0.04
8	S(reproductive condition +sex+site+ food+fire) $\Psi(\text{breeding season+ reproductive condition+sex+site+food*predation})$	44	4.66	0.04

Table 3-10. Model comparison table for multistate capture-mark-recapture analysis examining the effect of predation, feeding, and fire treatments on survival (S) and transition probabilities (Ψ , between reproductive and non-reproductive states) of oldfield mice in southwestern Georgia, between 2005 and 2009. All models had capture probability set at $p(\text{session})$. See Table 3-1 for column definitions. Bolded text indicates treatment effects (all other effects are similar between models throughout the set). Only models with a model weight > 0.03 are shown here (the top 9 models of 55 in the overall set).

Model no.	Model	K	ΔQAICc	Model weight
1	S(reproductive condition+site+ food*predation) $\Psi(\text{breeding season+reproductive condition +site})$	40	0.00	0.14
2	S(reproductive condition+site+ food+predation) $\Psi(\text{breeding season+reproductive condition+site})$	39	0.81	0.09
3	S(reproductive condition+site+ food*predation) $\Psi(\text{breeding season+reproductive condition+site+predation})$	41	1.29	0.07
4	S(reproductive condition+site+ food*predation) $\Psi(\text{breeding season+reproductive condition+site+food})$	41	1.69	0.06
5	S(reproductive condition+site+ predation*fire) $\Psi(\text{breeding season+reproductive condition+site})$	40	1.90	0.05
6	S(reproductive condition+site+ predation) $\Psi(\text{breeding season+reproductive condition+site})$	38	1.96	0.05
7	S(reproductive condition +site+ food+predation) $\Psi(\text{breeding season+reproductive condition+site+predation})$	40	2.10	0.05
8	S(reproductive condition+site+ food+predation) $\Psi(\text{breeding season+reproductive condition+site+predation})$	40	2.50	0.04
9	S(reproductive condition+site+ food+predation+fire) $\Psi(\text{breeding season+reproductive condition +site})$	40	2.66	0.04

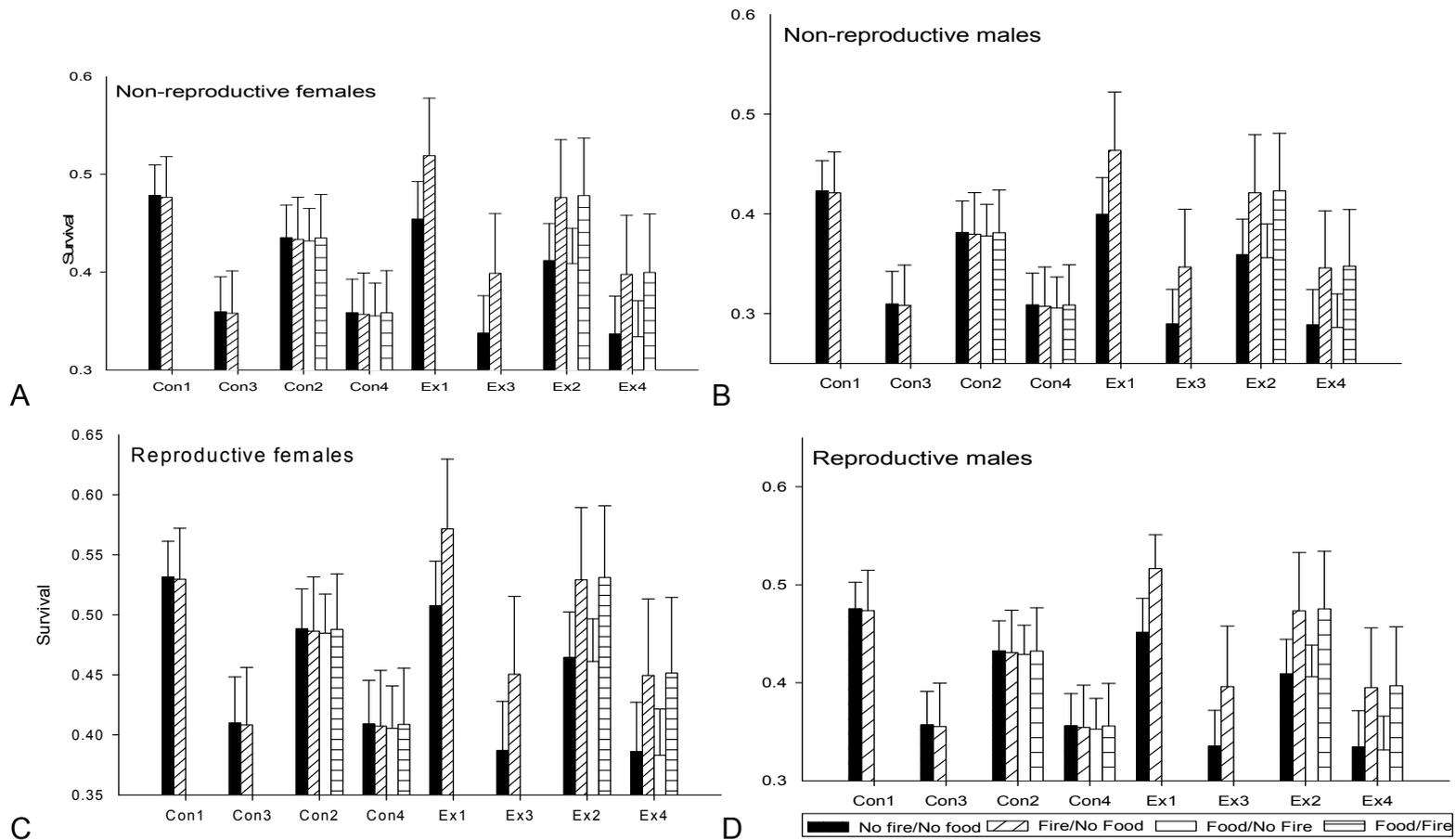


Figure 3-1. Model averaged estimates of survival of cotton mice in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and predator control treatments. Estimates are given for non-reproductive (A and B) and reproductive (C and D) male and female mice. Survival is estimated over 10 week intervals. Estimates are given by site: “Ex” sites refer to areas treated with mammalian predator exclusion and “Con” refers to mammalian predator access areas sites. Supplemental food was added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

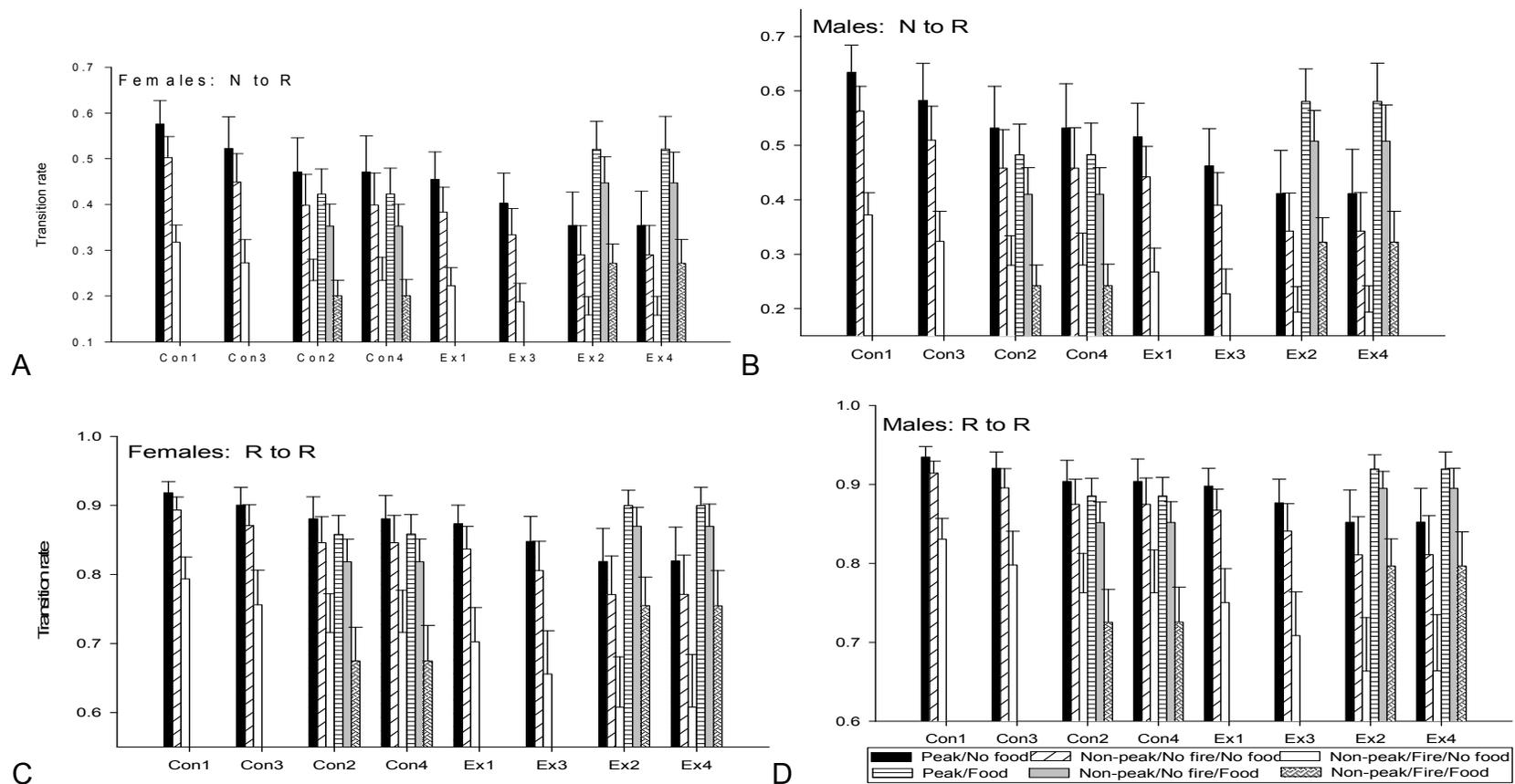


Figure 3-2. Model averaged estimates of breeding transitions for male and female cotton mice in southwestern Georgia between 2005 and 2009 during peak breeding seasons (fall and early winter), non-peak seasons during which burning did not occur and non-peak seasons during which burning did occur. Transitions include transition of non-reproductive individuals to reproductive states (N to R, A and B) and reproductive individuals staying in a reproductive state (R to R; C and D). Transitions occurred over 10 week intervals. Estimates are given by site: “Ex” refers to areas treated with mammalian predator exclusion; “Con” refers to mammalian predator access sites. Supplemental food was added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

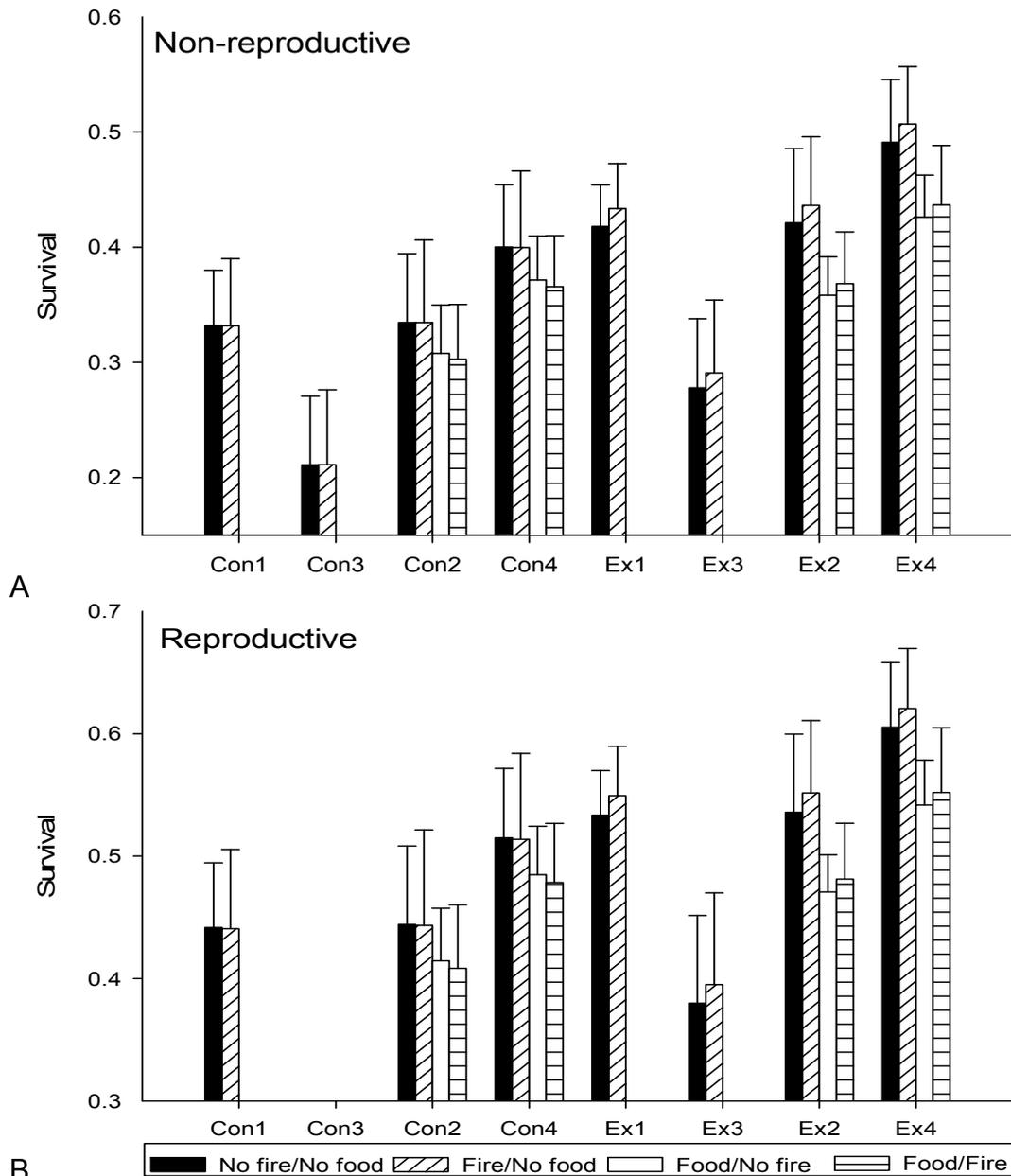


Figure 3-3. Model averaged survival estimates in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and predator control treatments. Estimates are given for non-reproductive (A) and reproductive (B) individuals. Survival is estimated over 10 week intervals. Estimates are given by site: “Ex” sites refer to areas treated with mammalian predator exclusion while “Con” sites refer to areas where mammalian predators were allowed access. Supplemental feeding treatments were added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

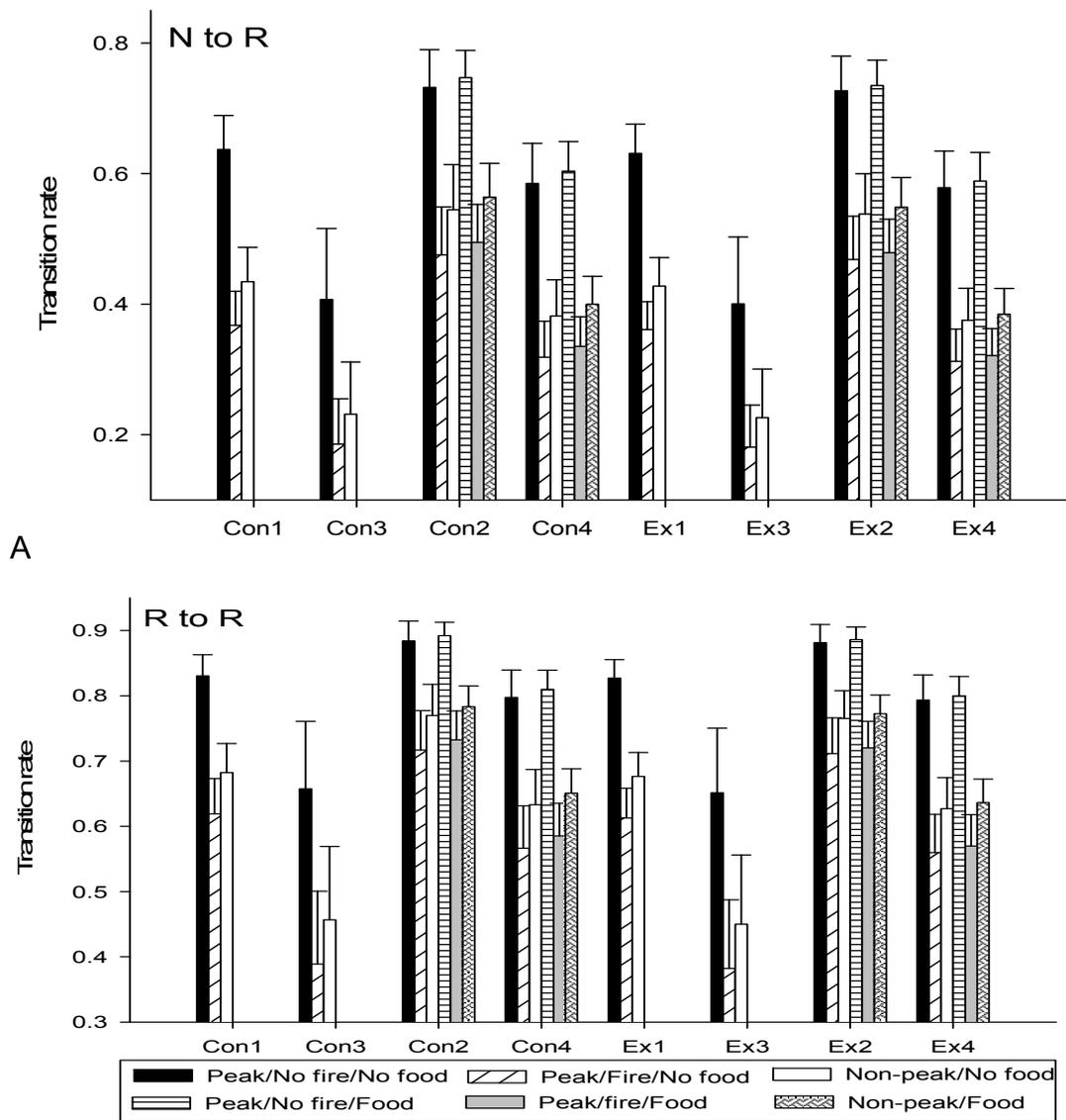


Figure 3-4. Model averaged estimates of breeding transitions for oldfield mice in southwestern Georgia between 2005 and 2009 during peak breeding seasons (winter and summer) in burn and non-burn years and non-peak breeding seasons. Transitions include non-reproductive individuals transitioning to reproductive states (N to R; A) and reproductive individuals staying in a reproductive state (R to R; B). Transitions are estimated over 10 week intervals. Estimates are given by site: “Ex” sites refer to areas treated with mammalian predator exclusion while “Con” sites refer to areas where mammalian predators were allowed access. Supplemental feeding treatments were added to Con and Ex sites 2 and 4 from summer 2007 through 2009. All sites were burned during the winters of 2005, 2007 and 2009.

CHAPTER 4 CONCLUSIONS

Although the three target species in this study, cotton rats, cotton mice, and oldfield mice occupy similar habitats, each showed different responses to supplemental feeding, predation, and prescribed fire treatments. Cotton rat populations were primarily driven by fire events, although food effects were apparent in non-fire periods, and likely would have become important in post-fire periods if predation and emigration had not caused rapid population declines. Although cotton rat mortality and turnover is primarily driven by predation, there was little evidence of direct, negative effects of mammalian predation on cotton rat survival and reproduction. However, we detected evidence that cotton rats behave adaptively in response to predation pressure as male rats had smaller home ranges in predator access grids compared to exclosures.

Of the three treatments applied here, oldfield mice were most strongly affected by predation. Predator access grids were associated with smaller abundances and lower survival. The observed effects occurred in the expected form and direction, indicating a negative effect from mammalian predation. However, lacking behavioral data, it is unclear whether these effects were consumptive or non-consumptive in nature. Although previous studies have demonstrated that oldfield mice generally exhibit a short-term neutral response to fire, probably due to their preference for areas that already have little cover, we found that prescribed burning had a negative impact on transitions to reproductive states for this species. We believe this may be due to changes in availability of preferred food sources such as insects.

Cotton mouse populations saw different treatment effects on the various population parameters. Food addition increased abundances. Survival increased in

predator exclusion grids following fires. Reproduction was positively influenced by the interaction of predator exclusion and food supplementation and negatively influenced by burning. These complex responses may result from behavioral responses to predation pressure. For example, following fires, when predation risk is high, cotton mice appear to make trade-offs in favor of survival at the expense of reproduction. However, as with oldfield mice, the understanding of this system would be improved if behavioral data were available to supplement the trapping data considered here.

There is a need for long-term, large-scale, replicated experiments to further address questions relating to interactions between predation and food resources, particularly in terrestrial systems. Such experiments would benefit from the incorporation of behavioral data with data regarding vital rates.

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BIOGRAPHICAL SKETCH

Gail Morris is originally from Williamsport, Pennsylvania. She attended Muhlenberg College in Allentown, PA and received a BS in Biology in 2004. Following a series of seasonal wildlife field jobs, she ended up at the Joseph W. Jones Ecological Research Center where, among other things, she caught and chased rats for a year. This led to the unexpected discovery of a fascination with rats, mice, and other critters at the bottom of the food chain. She was eventually offered a graduate assistantship with the University of Florida which enabled the continuation of rat and mouse studies at the Jones Center.