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Effects of predation, fire, and supplemental feeding on populations of two species of *Peromyscus* mice

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Food resources and predation play important roles in determining small mammal population dynamics. These factors also can interact as individuals under predation pressure make trade-offs between access to food resources and exposure to predators. Fires consume food sources and reduce cover, which increases exposure to predators. For species that occur in areas with frequent fire, it is instructive to consider how all of these factors interact to affect populations of interest. We examined how supplemental feeding, mammalian predator exclusion, and prescribed fire affected survival, abundance, and reproduction of cotton mice (*Peromyscus gossypinus*) and oldfield mice (*P. polionotus*) in a longleaf pine ecosystem. Burning and predator exclusion interacted to affect survival of cotton mice; survival was similar in predator exclosures and controls in nonburning periods and in controls following prescribed burns but increased in exclosures following burns. Rates of transitions to reproductive states (which for females includes lactation or gravidity and for males, descent of testes) decreased in burn years but increased with the combination of feeding and predator exclusion. Supplemental feeding increased abundances. Among oldfield mice, survival and abundance were greater in predator exclusion areas than in controls. Supplemental feeding and the interaction of feeding and predator exclusion also increased abundances. During peak breeding seasons during which burning occurred rates of transitions to reproductive states declined to such an extent that reproductive transition rates in these seasons were lower than during nonpeak breeding seasons.

Key words: cotton mouse, food supplementation, oldfield mouse, *Peromyscus gossypinus*, *Peromyscus polionotus*, predation, prescribed fire

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Factors that limit populations are often of interest to ecologists. Access to food resources and predation are common limiting factors. Food supplementation has been associated with increases in abundance, survival and reproduction, and changes in immigration rates (Boutin 1990; Hubbs and Boonstra 1997; Krebs et al. 1995; Taitt and Krebs 1983). Predator removal has been associated with increased densities, survival, immigration, and earlier breeding (Oli 2003; Perrin and Johnson 1999; Salo et al. 2010; Taitt and Krebs 1983). Effects of food availability and predation often are examined separately, but much evidence from theoretical and field studies suggests that these factors interact and should be considered simultaneously (Abrams 1982; Hubbs and Boonstra 1997; Krebs et al. 1995; McNamara and Houston 1987). Access to food resources is important to avoid starvation and is associated positively with reproduction, but the act of foraging often increases predation risk. Optimally, individuals should minimize predation risk while maximizing food intake. Such trade-offs can have impacts at the population level by influencing parameters such as survival, reproduction, and abundance (Lima and Dill 1989).

For the target species in this study, cotton and oldfield mice (*Peromyscus gossypinus* and *P. polionotus*, respectively), a 3rd factor might 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 (Smith 2000; 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 frequency of burning can influence the response (Masters 2007; Masters et al. 2002; Suazo et al. 2009). Most previous studies examining fire effects on small mammals have focused on short term (<1 year) effects on abundance. These studies have shown that cotton mice respond to fire either neutrally or with immediate but temporary population spikes in burned areas (Hatchell 1964; Layne 1974; Shadowen 1963; 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 determine experimentally mechanisms underlying population-level responses to fire, and few that have examined fire effects on a broader range of population parameters such as survival and reproduction.

The objective of this study was to examine experimentally the effects of supplemental feeding and mammalian predator exclusion on cotton and oldfield mouse populations. We also were interested in determining the contribution of these factors to population changes following prescribed burning. This was accomplished by establishing a large-scale factorial experiment with mammalian predator exclusion and supplemental feeding treatments applied over 4.5 years and through 3 burn cycles.

Based on results of previous field experiments that examined small mammal response to similar treatments and knowledge of the natural history of cotton and oldfield mice, we predicted that: abundance and rates of transition to reproductive states would increase in both species in response to supplemental feeding, mammalian predator exclusion, and the combination of these treatments; that feeding effects on population parameters would be greater in magnitude than predator exclusion effects; that prescribed burning would have a neutral effect on abundance and either a neutral or negative effect on survival of cotton mice; that given the preference of the oldfield mouse for open habitats, oldfield mice would show no strong response to burning and that response would not be influenced by food addition or mammalian predator exclusion; and that for both species, if any negative responses to burning occurred, these would be mitigated, at least in part, by mammalian predator exclusion, but not by food supplementation (i.e., we predicted that negative fire responses would be driven primarily by loss of cover and increased exposure to predators rather than food availability).

Materials and Methods

Study site and species.—This research was conducted at the Joseph W. Jones Ecological Research Center at Ichauway (hereafter Ichauway) in Baker County, Georgia (property located between 31.31°N and 31.16°N and 84.55°W and 84.36°W). 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 overstory, a diverse, herbaceous groundcover, and an open, park-like midstory (Van Lear et al. 2005). Hardwood tree species occur at low densities. Frequent, low-intensity fire is a key ecological process. Consequently, application of prescribed fire is a primary management tool throughout Ichauway; most sites are burned on a 2-year rotation.

Cotton and oldfield mice are common across the southeastern and south-central United States. The semiarboreal cotton mouse prefers bottomland hardwood forests but is a habitat generalist (Ivey 1949). Downed woody debris is an important microhabitat component for this species (McCay 2000). Oldfield mice prefer dry, open fields with loose soils. The species is noted for monogamous breeding habits (Blair 1951).

Field methods.—In 2002 the Jones Center constructed 4 mammalian predator exclosures, each approximately 40 ha and paired with a nearby control with similar habitat. Exclosures were surrounded by 1.2-m-tall woven wire fences that 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 entered exclosures, regular monitoring by track counts and thermal camera surveys indicated significantly fewer mammalian predators in exclosures than in controls (from July 2004 to August 2009 mammalian mesopredator detections were 11 times more frequent in controls compared to exclosures—Conner et al. 2010).

Each control and exclosure contained a 12 × 12 small mammal trapping grid with 15-m spacing between stations. Elevated trapping stations (24 stations) also were interspersed throughout each grid, attached to trees at heights of 1.5–2 m. Pairs of grids were trapped 4 times per year (once each season) from January 2005 through June 2007 and 8 times per year (twice per season) from July 2007 through June 2009 using Sherman live traps (model XLK; H. B. Sherman Traps, Inc., Tallahassee, Florida). A small amount of a granular insecticide (Talstar Nursery Granular Insecticide; FMC Corporation, Philadelphia, Pennsylvania) was sprinkled around each trap to prevent deaths of captured small mammals due to fire ants. New captures were marked individually with metal ear tags (National Band and Tag Company, Newport, Kentucky). Data recorded for all captures included location, species, sex, body mass, age (adult or juvenile, based on weight), reproductive condition (for males, testes descended or not; for females, gravid or lactating, or both, or not), and hind-foot measurement.

In June of 2007, 2 exclosure and 2 control grids were selected randomly to receive a supplemental feeding treatment consisting of placing 113 g (4 ounces) of commercial rabbit chow in cans at every other station on the trapping grids. Food was replaced every other week. Empty cans were placed on the nonfeeding grids to mitigate any effects relating to the presence of the cans themselves (for example, providing refugia). 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 (Morris et al. 2010). We found no evidence that cans were defended by individuals of any species. This assessment was based on regular observations of cans being visited by multiple species and by multiple individuals of the same species (individuals were distinguished based on coloration, body size, and presence or absence of ear tags).

In February 2005, 2007, and 2009 all plots were burned according to Ichauway's burn plan, which has these study areas on a 2-year burn rotation. Trapping and handling methods followed recommendations of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Florida Institute of Food and Agricultural Sciences Animal Research Committee (approval number 003-07WEC).

Statistical methods.—Data considered for our analyses included capture–mark–recapture data for cotton and oldfield mice trapped between January 2005 and June 2009 (26 sessions, each 4 days long). Analyses were carried out in several stages. First, treatment effects on survival and transitions to reproductive states were assessed using multistate models in the R 2.9.1 (R Development Core Team 2009) package RMark (Laake and Rexstad 2008) to build models for program MARK (White and Burnham 1999). Robust design models implemented in program MARK were used to generate abundance estimates. Treatment effects on abundance were assessed using a repeated-measures analysis of variance (ANOVA).

Multistate capture–mark–recapture models were used to estimate and model state-specific survival (S), capture probability (p), and probability of transition between states (Ψ). States used for S and Ψ were based on reproductive condition. Females were considered to be in a reproductive state if, during a trapping period, they were found to be lactating or gravid, and males were considered reproductive if testes were descended. Individuals were considered to be in a nonreproductive state if these characteristics were not present. Models evaluating effects of reproductive condition on S estimate and model survival separately for reproductive and nonreproductive individuals. Models evaluating effects of reproductive condition on Ψ estimate and model probability that nonreproductive individuals transitioned to reproductive states, and probability that reproductive individuals remained in reproductive states (hereafter the phrases ''transitions to reproductive states'' and ''reproductive transitions'' will refer to both nonreproductive individuals transitioning to a reproductive state and reproductive individuals remaining reproductive together). Assessment of goodness-of-fit was carried out using the median $\hat{c}$ approach in program MARK (using the most-parameterized model that estimated most parameters—White and Burnham 1999). The median $\hat{c}$ indicated a mild overdispersion ($\hat{c} = 1.321$ for cotton mice and $\hat{c} = 1.339$ for oldfield mice); these estimated $\hat{c}$ values were used for quasilikelihood adjustments. After quasilikelihood adjustments, models in each parameter's set were compared using Akaike's information criterion corrected for small sample size (QAIC$_c$). Models were considered well supported if they had a $\Delta\text{QAIC}_c \leq 2$. The best-supported model within each parameter's set was selected as a base for modeling that parameter in further analyses.

Preliminary analyses considered the potential influence of trapping session, season (as traditionally defined), and year on p. Influences of reproductive condition and sex were assessed for S and Ψ. Breeding season (see below) also was 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 subsequently Ψ then were considered in a similar fashion. These preliminary analyses indicated that reproductive condition and sex, modeled in an additive fashion, were important factors for describing S in cotton mice (Appendix, Table S1, model 5; http://ufdc.ufl.edu/AA00001642/00001/pdf), and reproductive condition was important for oldfield mice (Appendix, Table S2, model 5; http://ufdc.ufl.edu/AA00001642/00001/pdf). For both species capture probability was best described as fully time varying (Appendix, Table S1, model 1 for cotton mice; Appendix, Table S2, model 1 for oldfield mice; http://ufdc.ufl.edu/AA00001642/00001/pdf).

To model Ψ we first investigated breeding season effects on Ψ. Because a literature review did not give a clear indication of when peak breeding seasons for these species occur in southwestern Georgia, we constructed a model set based on the literature (Suazo et al. 2009; Whitaker and Hamilton 1998; Wolfe and Linzey 1977) and personal observations to identify the peak breeding seasons. This analysis indicated that for cotton mice breeding peaked in fall and early winter (Appendix, Table S3, model 1; http://ufdc.ufl.edu/AA00001642/00001/pdf), and for oldfield mice bimodal peaks occurred in winter and summer (Appendix, Table S4, model 1; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Because of a potential confounding effect of prescribed burning treatments and breeding seasons occurring as occasion-dependent effects, we then assessed whether evidence existed to support further division of cotton mouse nonbreeding seasons into whether a burn occurred during these seasons. Because the burns occurred during the oldfield mouse peak breeding season, a similar division was made, but with respect to peak breeding seasons rather than nonpeak seasons. Further division of breeding seasons based on burning was well supported (Appendix, Table S3, model 7 for cotton mice, and Appendix, Table S4, model 5 for oldfield mice; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Using these breeding season models, which included consideration of burn and nonburn years, 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 (Ψ(reproductive condition + sex + breeding season), Appendix, Table S1, model 10; http://ufdc.ufl.edu/AA00001642/00001/pdf), and reproductive condition and breeding season, also modeled in an additive fashion, were important for oldfield mice (Ψ(reproductive condition + breeding season), Appendix, Table S2, model 10; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Although the prescribed fires occurred at specific times, fire-caused changes in cover and food resources can 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 among all trapping periods except those following fires. Postfire survival was allowed to vary over several different intervals; for example, from the interval during which fire occurred (13 weeks postfire in 2005 and 2007 and 7 weeks postfire in 2009) and through multiple additional intervals across the summer season (39 weeks) when vegetation typically recovered. For both species no single model had overwhelming support (Appendix, Table S5; http://ufdc.ufl.edu/AA00001642/00001/pdf). 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 10 weeks (Appendix, Table S5, model 1; http://ufdc.ufl.edu/AA00001642/00001/pdf). For oldfield mice the best-supported model indicated an effect lasting 30 weeks (Appendix, Table S5, model 5; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Exclosure and control sites initially were selected as pairs based on geographic proximity. These pairs also tend to have similar habitat characteristics. As part of a post hoc examination of base 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 2nd set of models considering paired site effects on S and Ψ. This analysis indicated that paired site effects were important in modeling both S and Ψ for cotton and oldfield mice (Appendix, Table S6, model 1 for cotton mice and model 5 for oldfield mice; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Treatment effects were added to the best base model—for cotton mice: S(reproductive condition + sex + site) p(session)Ψ(breeding season + reproductive condition + sex + site), and for oldfield mice: S (reproductive condition + site) p(session)Ψ(breeding season + reproductive condition + site)—as additive and interactive effects (2-way only). Due to confounding effects relating to both fire and breeding season occurring as occasion-dependent effects, only supplemental feeding and predation treatments were considered with respect to Ψ, and supplemental feeding, predation, and fire effects were considered with respect to S. Model-averaging, which weights parameter estimates using normalized QAIC$_c$ model weights (Anderson 2008), was employed to generate model averaged estimates of S and Ψ. Averaging was carried out using the entire model sets, which were balanced for all treatments.

Abundance estimates (N) also were generated for both species. Pollock's robust design (Pollock 1982) was used for cotton mice. Because of problems with convergence, 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 models was similar to that used for the multistate capture–mark–recapture analysis. Preliminary analysis investigated effects of time and sex on p and c. Paired-site effects were considered for N (population size). S was modeled using the best-supported S model from the multistate analysis—without reproductive condition: S(sex + site + fire*predation). The γ terms were modeled using a random emigration effect [$\gamma''(.) = \gamma'(.)$].

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 also was important for modeling capture–recapture probabilities—p(session + sex)c $(p + c')$ where c' is the constant trap-happy response (Appendix, Table S7, model 3; http://ufdc.ufl.edu/AA00001642/00001/pdf). Paired-site effects were important for N (Appendix, Table S7, model 1; http://ufdc.ufl.edu/AA00001642/00001/pdf).

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(sex + site + fire*predation)$\gamma''(.) = \gamma'(.)p$(session + sex)$c(p + c')N$(site)—was used to estimate abundance as derived parameters by site and session but not to assess treatment effects. Treatment effects on abundance were evaluated using a repeated-measures ANOVA with the PROC MIXED procedure in SAS (SAS Institute Inc. 2004; Schabenberger and Pierce 2002). ANOVA assumptions, including equal variance and normality, were checked by examining plots of residuals and normal probability plots. Fixed effects considered in this ANOVA included food, fire, and predation treatments and their interactions (2-way interactions only). Paired sites were included as a random effect. Multiple covariance structures were investigated, and the best covariance structure was selected based on Akaike's information criterion adjusted for small sample size (AIC$_c$) value (Miller et al. 2004). The variance components structure (which allows a different variance for each random effect) was used because, for both *Peromyscus* species, it was the only covariance structure with a ΔAIC$_c$ value $\leq$ 2. Other covariance structures considered in the candidate model set included compound symmetry, banded Toeplitz, and 1st-order autoregressive structures. 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 structure of 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; Φ(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 based on ΔAIC$_c$. 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, and N was best modeled varying by site (Appendix, Table S8; http://ufdc.ufl.edu/AA00001642/00001/pdf).

The resulting model—Φ(predation)p(year + season)$pent$(year + season)N(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 2,108 individual cotton mice (8,428 total captures) was trapped over 26 trapping sessions in 8 plots. The best-supported multistate model suggested an interactive effect of predation and fire treatments on survival, with an interactive effect of supplemental feeding and predation on Ψ (Table 1, model 1; for the full AIC table see Appendix, Table S9; http://ufdc.ufl.edu/AA00001642/00001/pdf). Although this model was the best supported (the 2nd-ranked model had a $\Delta QAIC_c > 2$), the AIC_c weight associated with the model was only 0.393. However, it was clear from the top-ranked models that supplemental feeding interacted with predation to affect Ψ. This interaction appeared in the top 10 (of 55) 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 2nd-best-supported model (Table 1, model 2) included no treatment effect on survival, indicating poor support for treatment effects other than an interactive effect of predation and fire.

The lack of substantial support for any particular model indicates model selection uncertainty; therefore, model-averaging was used to estimate survival. Overall model-averaged survival estimates showed that males had lower survival than females and that reproductive individuals had higher survival than nonreproductive individuals (Fig. 1; see Appendix, Fig. S1, for estimates for all sites; http://ufdc.ufl.edu/AA00001642/00001/pdf). Model-averaged estimates indicated that in predator controls burning had essentially no effect on survival. In predator exclosures, however, survival increased following fires (Fig. 1). During nonburn periods survival was slightly greater in predator controls than in the exclosures, but this trend was reversed following burns (Fig. 1). The addition of food had minimal impact on survival, regardless of whether predators had access or an area had been burned recently (Fig. 1).

Model-averaged parameter estimates for Ψ showed that males entered reproductive states (including both nonreproductive individuals becoming reproductive and reproductive individuals remaining reproductive) at greater rates than females (Fig. 2; see Appendix, Fig. S2 for estimates for all sites; http://ufdc.ufl.edu/AA00001642/00001/pdf). Most reproductive individuals remained reproductive; this trend was slightly greater for males than females (Fig. 2). Initial investigation indicated a strong fire effect on transitions to reproductive states: models that included 3 classes of breeding seasons—peak breeding in fall and early winter; nonpeak breeding in springs, summers, and late winters without burns; and a separate nonpeak in springs, summers, and late winters of burn years (hereafter, peak, nonpeak/nonburn, and nonpeak/burn, respectively)—had overwhelming support over models with only 2 types of breeding seasons (peak and nonpeak with no distinguishing between burn and nonburn years; Appendix, Table S3; http://ufdc.ufl.edu/AA00001642/00001/pdf). Model-averaged parameter estimates indicated that transitions to reproductive states were at their greatest during peak breeding seasons, with a small drop in transitions to reproductive states during nonpeak/nonburn seasons (Fig. 2). Transitions to reproductive states dropped considerably more during nonbreeding/burn seasons (Fig. 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 (Fig. 2).

Supplemental feeding had an effect on abundance ($F_{1,195} = 20.91$, $P < 0.001$). Examination of least-square means indicated that feeding plots contained 1.8 times the number of cotton mice as unfed plots. Predation and fire treatments, and interactions of predation, fire, and feeding treatments had no significant effects on abundance ($F_{1,195} \leq 1.39$, $P \geq 0.24$).

Oldfield mice.—A total of 1,203 individual oldfield mice (4,828 total captures) was trapped over 26 trapping sessions in 8 trapping plots. No clear best-supported multistate model was generated for oldfield mice, because 6 models had a $\Delta QAIC_c < 2$, none of these carrying much weight (Table 2; see Appendix, Table S10 for full AIC table; http://ufdc.ufl.edu/AA00001642/00001/pdf). However, it was clear from the top-ranked models that predation was an important factor affecting survival. Predation effects appeared in the top 20 (of 55) models, and these models collectively held 82.8% of the weight of the model set. Models including a feeding effect also had reasonable 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 used to estimate reproductive state.

Model-averaged survival estimates indicated that nonreproductive individuals had lower survival than reproductive individuals (Fig. 3; see Appendix, Fig. S3 for estimates for all sites; http://ufdc.ufl.edu/AA00001642/00001/pdf). Model-averaged survival estimates also showed increased survival in predator exclusion plots compared to predator controls. This was true in both pre- and postfire periods. Following prescribed fires, survival decreased slightly in predator access grids and increased (by a slightly greater magnitude) in predator exclosure treatments (Fig. 3). Addition of food was associated with declines in survival in both predator access and exclosure grids, and in both pre- and postfire periods. The magnitude of the decline was greater in exclosures than in controls, but the magnitude of the change was not great in either case.

Initial investigation indicated strong fire effects on transitions to reproductive states: models that included 3 classes of breeding seasons (bimodal peak breeding in winters and summers, distinguishing between burn years

TABLE 1.—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 nonreproductive states for cotton mice in southwestern Georgia, 2005–2009. All models had capture probability set at *p*(session). Table includes number of parameters (*K*), difference in Akaike's information criterion corrected for small sample size after quasilikelihood adjustment ($\Delta QAIC_c$), and model weights (ω, relative likelihood of models in the set). Quasilikelihood adjustments were made using an estimated $\hat{c}$ (goodness-of-fit—White and Burnham 1999) of 1.321. Boldface text indicates treatment effects (all other effects are similar among models throughout the set). Only models with a model weight > 0.03 are shown here (the top 8 models of 55 in the overall set). See Appendix, Table S9 for full table, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

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

and nonburn years, and nonpeak breeding in falls and springs) had overwhelming support over models with only 2 types of breeding seasons (peak and non peak, with no distinction between burn and nonburn peak seasons; Appendix, Table S4; http://ufdc.ufl.edu/AA00001642/00001/pdf).

Model-averaged parameter estimates for Ψ indicate that the majority of reproductive individuals remained reproductive

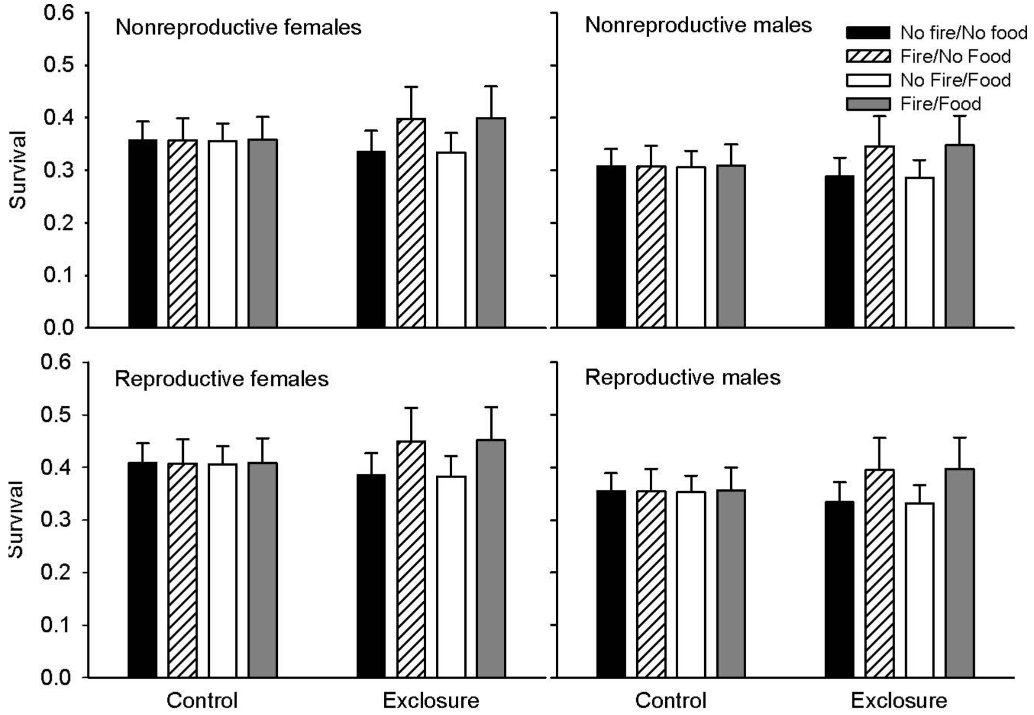

FIG. 1.—Model-averaged estimates (± *SE*) of survival of cotton mice in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and predator control treatments. Estimates were generated using multistate capture–mark–recapture models. Survival was estimated over 13-week intervals. Estimates are given for representative sites: Exclosure indicates mammalian predator exclusion, and Control indicates mammalian predator access. See Appendix, Fig. S1 for estimates for all sites, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

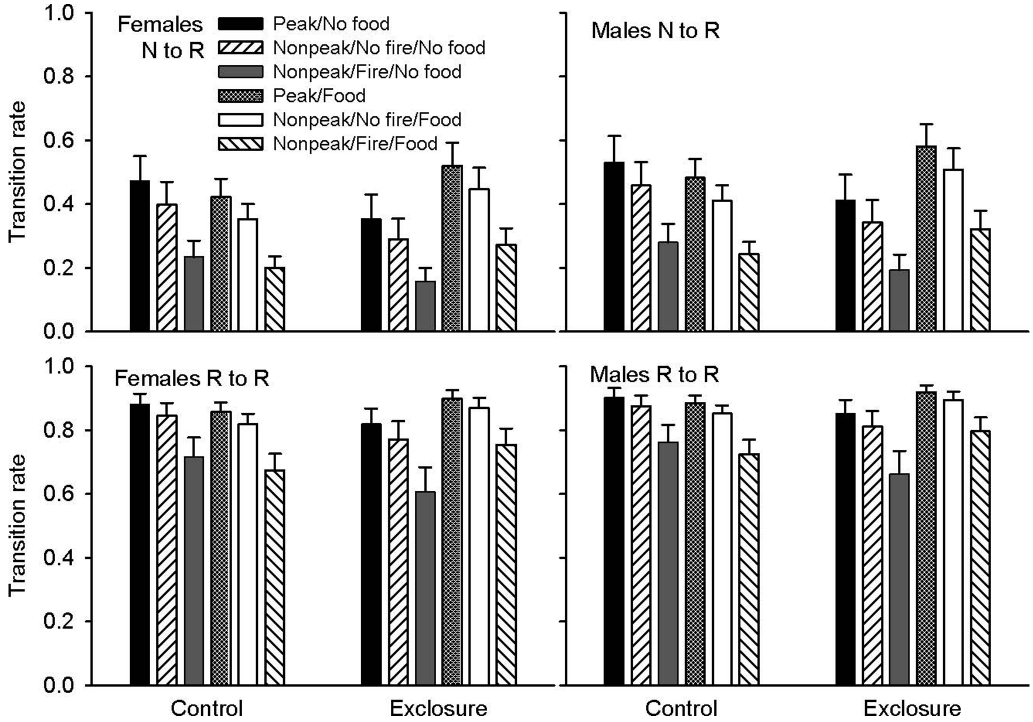

Fig. 2.—Model-averaged estimates (± *SE*) of reproductive transitions for cotton mice in southwestern Georgia between 2005 and 2009 during peak breeding seasons (fall and early winter), nonpeak seasons during which burning (prescribed fire) did not occur, and nonpeak seasons during which burning did occur. Transitions include nonreproductive individuals entering reproductive states (N to R) and reproductive individuals remaining reproductive (R to R). Estimates were generated using multistate capture-mark-recapture models. Transitions occurred over 13-week intervals. Estimates are given for representative sites: Exclosure indicates mammalian predator exclusion, and Control indicates mammalian predator access. See Appendix, Fig. S2 for estimates for all sites, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

(Fig. 4 shows estimates for a representative pair of sites; see Appendix, Fig. S4 for estimates for all sites; http://ufdc.ufl.edu/AA00001642/00001/pdf). Transitions to reproductive states (both nonreproductive individuals becoming reproductive and reproductive individuals remaining reproductive) were the greatest during peak breeding seasons of nonburn years. Transitions into breeding states dropped during nonpeak seasons. However, during peak breeding seasons of burn years,

Table 2.—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 nonreproductive states for oldfield mice in southwestern Georgia, between 2005 and 2009. All models had capture probability set at p(session). See Table 1 for column definitions. Quasilikelihood adjustments were made using an estimated $\hat{c}$ (goodness-of-fit—White and Burnham 1999) of 1.339. Boldface text indicates treatment effects (all other effects are similar among 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). See Appendix, Table S10 for full table, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

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

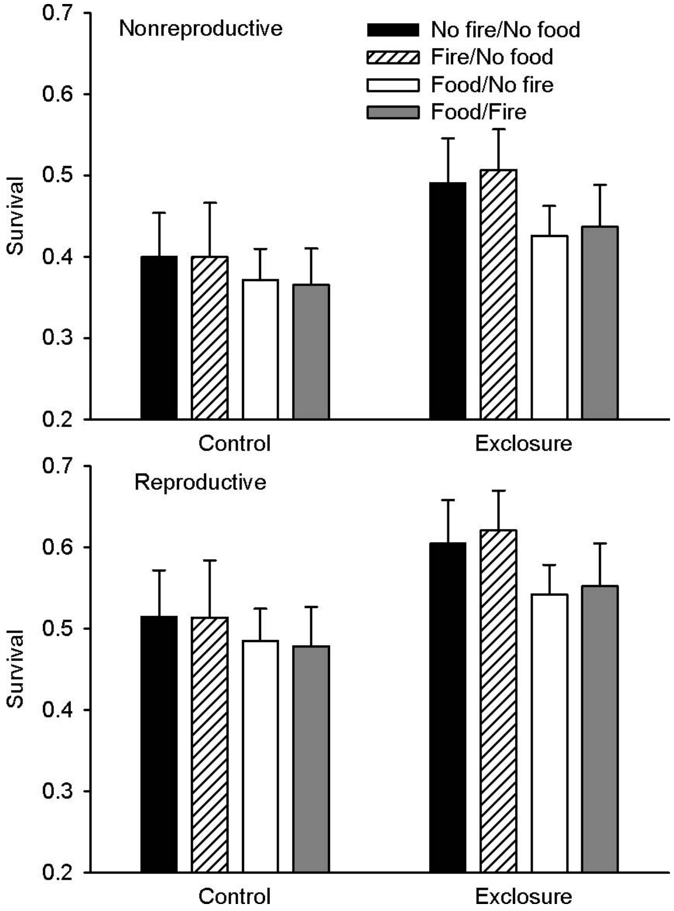

Fig. 3.—Model-averaged estimates (± *SE*) of survival of oldfield mice in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and predator control treatments. Estimates were generated using multistate capture–mark–recapture models. Survival was estimated over 13-week intervals. Estimates are given for representative sites: Exclosure indicates mammalian predator exclusion, and Control indicates mammalian predator access. See Appendix, Fig. S3 for estimates for all sites, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

transitions to breeding states dropped dramatically such that transitions during these seasons were below even that of nonbreeding seasons, indicating a strong negative fire effect on reproduction in oldfield mice (Fig. 4).

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

Predation and feeding treatments interacted to have a significant effect on abundance ($F_{1,187} = 12.64$, $P = 0.001$). Examination of least-square means showed that feeding increased abundances by 2.7 times, predator exclusion increased abundances by 2.7 times, and the application of both treatments simultaneously increased abundances by 7.6 times. The fire treatment and interactions of fire with predation or feeding treatments had no significant effects on abundance ($F_{1,187} \leq 3.20$, $P \geq 0.08$).

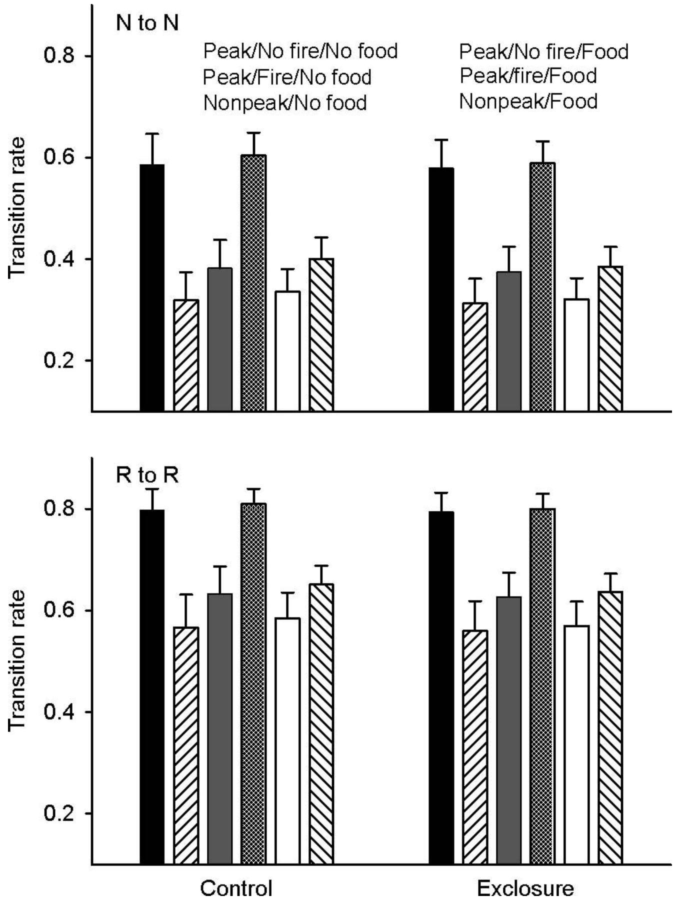

Fig. 4.—Model-averaged estimates of reproductive transitions (± *SE*) for oldfield mice in southwestern Georgia between 2005 and 2009 during peak breeding seasons (winter and summer) in burn (prescribed fire) and nonburn years and nonpeak breeding seasons. Transitions include nonreproductive individuals entering reproductive states (N to R) and reproductive individuals remaining reproductive (R to R). Estimates were generated using multistate capture–mark–recapture models. Transitions were estimated over 13-week intervals. Estimates are given for representative sites: Exclosure indicates mammalian predator exclusion, and Control indicates mammalian predator access. See Appendix, Fig. S4 for estimates for all sites, at http://ufdc.ufl.edu/AA00001642/00001/pdf.

Discussion

Cotton and oldfield mice are closely related species that occur in many of the same habitats, but they were affected differently by mammalian predator exclusion, supplemental feeding, and prescribed fire treatments. However, both species showed a surprising trend of increased survival among reproductive individuals compared to nonreproductive individuals. We hypothesize that this is because nonreproductive adults are likely to be younger individuals. Although some evidence suggests that reproduction exacts a survival cost among small mammals (Koivula et al. 2003), the cost of being young might be greater among these mice. 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 is adaptive in general if dispersal improves reproduction (Van Vuren and Armitage 1994). Alternatively, this effect could be due to confounding that occurs in capture–mark–recapture analyses between death and permanent emigration. It is possible that the observed lower survival of nonreproductive individuals resulted from higher rates of permanent emigration among nonreproductive compared to reproductive individuals.

Initial analyses identified sex as an important factor with respect to both survival and reproductive transitions of cotton mice, but among oldfield mice, sex effects were poorly supported. This could be related to the breeding strategies of these mice; oldfield mice are monogamous and form long-term pair-bonds, and cotton mice are promiscuous (Blair 1951).

Treatment effects on cotton mice.—Cotton mice showed different treatment effects on different vital rates. As predicted, and as has been observed with other mammalian species (Boutin 1990), food addition increased abundances; however, no similar increase in abundance was observed in response to mammalian predator exclusion. Neither feeding nor predator exclusion influenced survival. Following burns, survival increased in predator exclosures, but survival was similar across all treatments and controls at all other times. Fire had a negative effect on transitions to reproductive states, but it is unclear if this effect was due to fire-caused changes in cover or food availability because feeding and predation treatments did not influence the response.

Manipulation of predators influences survival and abundance of other small mammal species, including snowshoe hares, voles, and arctic ground squirrels (Desy and Batzli 1989; Hubbs and Boonstra 1997; Krebs et al. 1995). Previous studies examining roles of predation and food availability on small mammal populations have indicated that food availability more strongly influences population dynamics than does predator exclusion or removal (Desy and Batzli 1989; Hubbs and Boonstra 1997; Krebs et al. 1995). This pattern was observed in our experiment as well, but we did not expect a near-complete absence of predator exclusion effects. A review of predator manipulation experiments (Salo et al. 2010) suggests that the results of such experiments depend largely on the efficacy of predator manipulation. We are confident that the mammalian predator exclusion treatment was effective in greatly reducing mammalian predator populations in the exclusion grids, but raptors and snakes were not excluded, both of which contribute to cotton mouse mortality (Blair 1951; Whitaker and Hamilton 1998). Raptors contribute more significantly than mammalian predators to the mortality of another rodent in our study area, the cotton rat (Wiegert 1972). It is possible that a similar situation occurred with cotton mice, but we do not have adequate data to test this possibility. Alternatively, cotton mice might make behavioral adaptations to predation risk to mitigate negative effects of predation, but we lack the behavioral data necessary to evaluate this as well.

Food addition was associated with a nearly 2-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 also was not 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 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.

Many responses of the cotton mouse were unexpected or counterintuitive, or both. Some of the results observed here might not reflect direct responses to the treatments. Cotton mice occur in ecosystems populated by multiple other small mammal species, many of which occur in the same habitats. These species also responded to our experimental treatments in a variety of ways. The responses of oldfield mice are described in the ‘‘Results’’ and below. A common and aggressive species in our study areas, the cotton rat, responded to the feeding treatment with increased abundances but declined to near 0 following fires (Morris 2010). Such effects on sympatric species in the community could have influenced responses of the cotton mouse indirectly. Postfire increases in survival of the cotton mouse might have been related to declines in the cotton rat population, although if such is the case, the response appears to have been mitigated by the presence of mammalian predators. This sort of indirect effect was observed in a study that examined effects of predator exclusion on white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*—Yunger 2004). White-footed mice were affected negatively by predator exclusion (Yunger 2004), but this effect was likely not a direct response to the predator treatment itself but appears to have been in response to increased densities of meadow voles (Yunger 2004).

Treatment effects on oldfield mice.—Oldfield mice were affected most strongly by mammalian predator exclusion; this treatment was associated with increased survival and abundance. Feeding and predator exclusion interacted to increase abundance. These results were consistent with our predictions, but we did not detect feeding effects on survival or transitions to reproductive states.

Mammalian predation effects on oldfield mice were stronger than for cotton mice. Lacking data on cause-specific mortality for both species, it is difficult to determine the role of mammalian predation as compared to predation from raptors and snakes. However, it seems likely that mammalian predators contribute more to oldfield mouse than to cotton mouse mortality.

Fire had a negative effect on transitions to reproductive states during a peak breeding season. Given the preference of the oldfield mouse for open areas (Blair 1951), we did not expect to see strong fire effects on any population parameter. Food addition and mammalian predator exclusion were apparently insufficient to prevent such declines. Sufficient food quality and quantity are necessary for small mammals to achieve reproductive status (Cameron and Eshelman 1996). Trail camera observations of food cans showed that oldfield mice did use the supplemental food, but oldfield mice tend to consume insects and seeds more than herbaceous material (Gentry and Smith 1968). Although supplemental food was available following fires, other preferred food sources might have become limiting. For example, Odum et al. (1973) observed declines in arthropod abundances following a winter burn in Georgia for several months. Similar to the results observed with cotton mice, feeding was associated with increases in abundance but with only marginal increases in transitions to reproductive states, indicating that the feeding effect on abundance could be due to increases in immigration, juvenile survival, or the number of young produced per reproductive event.

Although cotton and oldfield mice are closely related species that occur in similar habitats, feeding, fire, and predation treatments affected these species differently. Studies incorporating cause-specific mortality and behavioral components such as space use, microhabitat use, and giving-up densities for foraging animals likely would improve our understanding of the population-level influence of the experimental treatments considered here.

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