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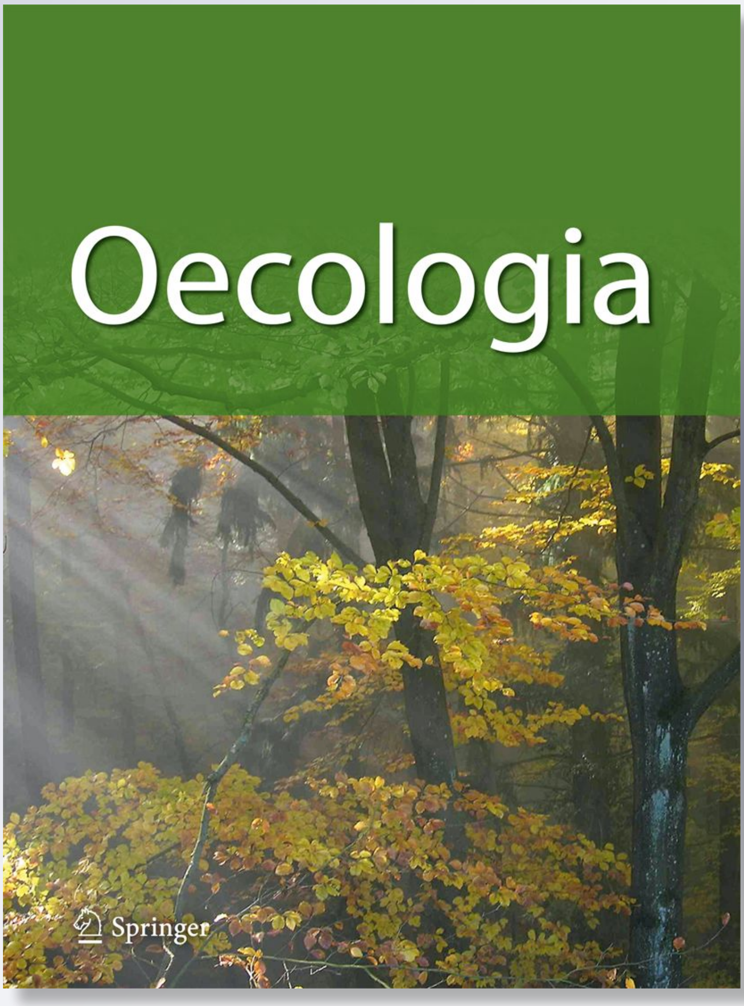
Oecologia

ISSN 0029-8549
Volume 167
Number 4

Oecologia (2011) 167:1005-1016
DOI 10.1007/s00442-011-2053-6



Springer

Oecologia (2011) 167:1005–1016
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POPULATION ECOLOGY - ORIGINAL PAPER

Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations

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Received: 10 September 2010 / Accepted: 23 May 2011 / Published online: 26 June 2011

Abstract Predation and food resources can strongly affect small mammal population dynamics directly by altering vital rates or indirectly by influencing behaviors. Fire may also strongly influence population dynamics of species inhabiting fire-adapted habitats because fire can alter food and cover availability. We used capture–mark–recapture and radio-telemetry studies to experimentally examine how supplemental feeding, mammalian predator exclusion, and prescribed fire affected survival, abundance, and reproduction of hispid cotton rats (*Sigmodon hispidus*) in southwestern Georgia, USA. Prescribed fire reduced survival, abundance, and rates of transitions to reproductive states. Food supplementation increased survival, transitions to reproductive states, and abundance, but was not sufficient to prevent post-fire declines in any of these parameters. Mammalian predator exclusion did not strongly affect any of the considered parameters. Our results show that fire strongly influenced cotton rat populations in our study site, primarily by reducing cover and increasing predation risk from non-mammalian predators.

Communicated by Peter Banks.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2053-6) contains supplementary material, which is available to authorized users.

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Keywords Demography · Longleaf pine · Multistate capture–mark–recapture models · Population-level response to fire · *Sigmodon hispidus*

Introduction

Predation and access to food can have dramatic effects on small mammal populations. Food supplementation has been associated with increases in abundance and survival, changes in immigration and emigration rates, earlier reproduction, and increased litter sizes (Tiatt and Krebs 1983; Boutin 1990; Campbell and Slade 1995; Krebs et al. 1995; Hubbs and Boonstra 1997; Perrin and Johnson 1999). Predator removal has been associated with increased densities, survival, and immigration, and earlier breeding (Wiegert 1972; Tiatt and Krebs 1983; Perrin and Johnson 1999; Oli 2003; Arthur et al. 2004; Yunger 2004; Salo et al. 2010).

Predation may also have sub-lethal effects relating to perceived predation risk. These include behavioral changes such as reduced activity, changes in habitat use, decreased home range size, and delayed age of first reproduction or onset of a breeding season (Lima and Dill 1989). Non-lethal effects that may result from such behaviors include decreased individual growth rates, poorer body condition, and decreased reproductive output (Hik 1995; Peckarsky et al. 2008). However, predators do not always strongly influence their prey. In systems where a prey species supports multiple predators, a single predator species may have limited influence, particularly if other predators make a greater contribution to prey mortality (Salo et al. 2010).

Although food availability and predation may individually have large impacts, there is much support for interactions between these factors (Tiatt and Krebs 1983;

Abrams 1984; McNamara and Houston 1987; Desy and Batzli 1989; Hubbs and Boonstra 1997). These interactions stem from the relationship between food acquisition and predation risk. Foraging increases exposure to predators, so individuals must make trade-offs between the need to acquire food and the need to avoid being eaten. Similar trade-offs may occur with other behaviors such as seeking reproductive opportunities (Lima and Dill 1989; Clark and Mangel 2000).

For species such as the hispid cotton rat (*Sigmodon hispidus,* hereafter cotton rat), fires cause a crisis of both food and predation. Fires consume herbaceous vegetation that cotton rats require for cover from predators and which they use as a primary food source (Whitaker and Hamilton 1998). Previous studies have shown that cotton rat populations decline dramatically following fires (Layne 1974; Bock and Bock 1978), although the species benefits from frequent fire application over the long term (Rehmeier et al. 2005). While the long-term benefits are likely related to the maintenance of suitable habitat structure (Masters et al. 2002), the factors driving the short-term declines remain poorly understood. Explanations relating to changes in food resources (Bock and Bock 1978) or cover, and by extension predation (Arata 1959; Clark and Kaufman 1990), are generally hypothesized, but neither has been experimentally tested.

We examined the effects of predation and food availability on survival, reproduction, and abundance of cotton rats over 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 also examined the roles of food availability and mammalian predation in cotton rat declines following prescribed fires.

Materials and 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 trees occur at low densities, and frequent, low intensity fire is a key ecological process. Application of prescribed fire is a primary management tool on Ichauway; most sites are burned every other year (Atkinson et al. 1996).

Cotton rats are solitary rodents found abundantly across the southeastern and south-central United States. Cotton rats are generally described as crepuscular, but they may be active throughout the day and night. They occur in many habitats but require thick cover, particularly in the form of dense grasses and shrubs (Goertz 1964), which provide protection from a wide range of avian, mammalian, and snake predators. Herbaceous vegetation is also a primary food source.

Experimental design

In 2002, the Jones Center constructed four mammalian predator exclosures and established four controls with similar habitat, each approximately 40 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 to pass through). Predators excluded include bobcats (*Lynx rufus*), coyotes (*Canis latrans*), grey foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), and nine-banded armadillos (*Dasypus novemcinctus*). Raptors and snakes had access to all sites. Mammalian predator presence in controls and exclosures was monitored regularly with track counts and thermal camera surveys. From July 2004 to August 2009, mammalian predator detections were 11× more frequent in controls than in exclosures (Conner et al. 2010). When mammalian predators were detected in exclosures, traps were set to remove them. These surveys indicate that, although mammalian predators occasionally entered exclosures, the exclosures significantly reduced mammalian predator abundances.

In February of 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. Post-fire evaluation determined that, on average, less than 10% vegetative fuel remained unburned. In the 2009 burn, during and after which radio-collared cotton rats were tracked intensively (see below), less than 5% vegetative fuel remained unburned.

From June 2007 through August 2009, 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 (Manna Pro Select Series Pro Formula, Chesterfield, MI, USA) in cans at every other station on trapping grids in selected sites (see below). Food was replaced every other week. Empty cans were placed on non-feeding grids to mitigate any effects relating to the presence of the cans themselves. 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. This assessment was based on regular observations of cans being visited by multiple species and by multiple individuals of the same species. For a discussion on the number of additional cotton rats the feeding treatment is likely to have supported, see the Electronic Supplementary Materials (ESM) Appendix S1.

Field methods

Each control and exclosure contained a 12 × 12 small mammal trapping grid with 15-m spacing between stations (total grid area of 3.24 ha; cotton rat home ranges averaged 0.36 ha for females and 0.63 ha for males, with substantial home range overlap; Morris 2010). 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 June 2009 using Sherman live traps (H.B. Sherman Traps, Tallahassee, FL, USA). A small amount of a granular insecticide (Talstar Nursery Granular Insecticide, FMC Corporation, Philadelphia, PA, USA) 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, mass, age (adult or juvenile, based on body mass; we considered cotton rats $\geq$50 g to be adults; Bergstrom and Rose 2004), reproductive condition (for males, testes descended or not, and for females, pregnant and/or lactating or not), and hind foot measurement.

From July 2007 through August 2009, 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 were anesthetized with Isoflurane (Minrad, Bethlehem, PA, USA) and fitted with 4.5-g radio-collars (Advanced Telemetry Systems, Isanti, MN, 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, IL, USA), R-1000 (Communication Specialists, Orange, CA, USA), or R-2000 receivers (Advanced Telemetry Systems). When transmitters no longer being worn by rats were found, the location was searched for sign to classify the event as a slipped transmitter 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. If rats with missing signals could not be retrapped (i.e., loss of signal unlikely to be due to transmitter failure), searches for missing transmitters were undertaken to detect emigration or carrying off of transmitters by far-ranging predators.

Rats were located by homing to verify status as alive 1–2 days prior to burning. Signals were monitored during the burn and rats were located by homing immediately after the fire. For 7 days following the fire, rats were tracked twice daily. Rats surviving past 7 days were tracked daily for an additional 7 days. Regular monitoring (i.e., located by triangulation or homing three times per week and located visually once a week) was restored thereafter. Missing rats were searched for immediately to detect emigration.

Trapping and tracking 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).

Analysis of capture–mark–recapture data

Capture–mark–recapture (CMR) data considered for our analyses included 26 sessions from January 2005 through June 2009, each lasting 4 days. Analyses were carried out using the R 2.9.1 (R Development Core Team 2009) 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 one for radio-collared rats.

Multistate CMR models were used to estimate and model state-specific apparent survival (S; use of "apparent survival" reflects the inability of CMR analyses to distinguish between death and permanent emigration), capture probability (p), and transitions between reproductive states (Ψ), conditional on survival. States used for S and Ψ were based on reproductive condition. Models for S that included reproductive condition as an effect estimated and modeled apparent survival separately for reproductive and non-reproductive individuals; likewise, models for Ψ that included reproductive condition as an effect estimated and modeled probabilities that non-reproductive rats became reproductive, and that reproductive rats remained reproductive.

Preliminary investigations considered the potential influence of trapping session, season (spring, summer, fall, and winter, as traditionally defined), and year on p. Influences of reproductive condition and sex were assessed for

S and Ψ. Breeding season was also considered for Ψ (ESM, Appendix S2). 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 then Ψ were considered in a similar fashion.

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 ($\hat{c} = 1.262$); this estimated $\hat{c}$ was used for quasi-likelihood adjustments. Models in each parameter's set were compared using Akaike's information criterion corrected for small sample size (AICc), after quasi-likelihood adjustments (QAICc). 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 as a base for modeling that parameter in further analyses.

Details of additional preliminary analyses are described in the ESM, Appendix S2. These analyses identified peak breeding seasons in our region, determined the interval over which to consider the fire treatment to have had an effect (although burns occur at specific times, fire-caused changes in cover and food resources last much longer), and assessed the importance of site effects. These analyses indicated: breeding peaks in spring and summer with strong support for dividing non-breeding seasons into whether they occurred in burn or non-burn years (ESM, Table S2); a short-term fire effect on apparent survival with declines in survival occurring only over the interval during which the fire occurred (ESM, Table S3); and support for including a paired site effect for modeling S and Ψ (ESM, Table S4; a paired site effect was used because exclosures and controls were established as pairs based on proximity and paired sites tended to have more similar habitats with each other than non-paired sites. See Appendix S2 for details).

The preliminary analyses indicated that reproductive condition and sex, modeled in an interactive fashion, were important for describing S (ESM, Table S1, model 5). Capture probability was best described as varying by session. Although all parameters were estimable using this model, standard errors were large, indicating poor precision; therefore, this model 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 (ESM, Table S1, model 1). 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 (ESM, Table S1, model 10).

Treatment effects were added to the best base multistate model [$S(\text{reproductive condition} \times \text{sex} + \text{site})p(\text{year} + \text{season})\Psi(\text{breeding season} + \text{reproductive condition} + \text{sex} + \text{site})$] as additive and interactive effects (two-way only). Due to confounding effects relating to fire and breeding season occurring as occasion-dependent effects (because burns always occurred in non-peak breeding seasons), 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 CMR models (Pollock 1982) were used to generate abundance estimates (N). Robust design models estimate probabilities for apparent 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, as described above, were considered for N. S was modeled using the best supported S model from the multistate analysis [minus the reproductive state term, $S(\text{sex} + \text{site} + \text{food} + \text{fire})$]. The γ terms were modeled using a random emigration effect [$\gamma''(.) = \gamma'(.)$].

Preliminary analyses indicated that c and p varied by session (ESM, Table S5, model 3) and that a paired site effect (as described in Appendix S2) was important for modeling N (ESM, Table S4, model 1). Because of difficulties associated with modeling treatment effects on abundance directly (White 2002), the best supported robust design model indicated by the preliminary analysis [$S(\text{site} + \text{sex} + \text{food} + \text{fire})\gamma''(.) = \gamma'(.)p(\text{session})c(\text{session})$ $N(\text{site})$] was used to generate derived abundance estimates by site and session, but not to determine treatment effects. Treatment effects were evaluated using a repeated measures ANOVA (Schabenberger and Pierce 2002) implemented using the PROC MIXED procedure in SAS (SAS Institute 2004). The model for this ANOVA included food, fire, and predation treatments and their interactions (two-way interactions only, to allow clear interpretation of interactive effects). Paired sites were included as a random effect. Multiple covariance structures were investigated and the best (variance components structure, which allows variance to differ for each random effect) was selected based on AICc value (Miller et al. 2004). Treatment effects were considered significant at $\alpha \leq 0.05$.

Survival analysis using radio-telemetry data

Survival of collared rats was estimated using the PROC PHREG procedure in SAS (Allison 1995). PROC PHREG uses the Cox proportional hazard model (Cox 1972), which is a semi-parametric model which assumes independence of fate among individuals and which allows modeling survival as a function of covariates when fates of individuals are known. 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 1 week following collaring or that died due to handling-related causes were not considered in this analysis. Although this was intended to mitigate potential negative effects on survival associated with rats becoming accustomed to being collared, excluding all rats that lived less than 1 week is likely to create an upward bias of the survival estimate of those rats that lived longer than 1 week. Therefore, the first week of all rats considered for survival analysis was also censored. Rats whose signals were lost and rats that 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.

Results

Effects on apparent survival

Over 26 trapping sessions in eight trapping plots, 2,557 individual cotton rats (6,815 total captures) were trapped. The multistate analysis showed six models with a ΔQAICc < 2, none with overwhelming support over the others (Table 1; the full AIC table is shown in ESM, Table S6). It is clear from the top-ranked models that fire and supplemental feeding effects were important factors affecting apparent survival. Fire effects appeared in the top 30 models and these held 100% of the model weight of the set. Food effects appeared in the top 14 models and these carried 92.5% of the model set's weight. There was no evidence that supplemental feeding or predator exclusion influenced Ψ. The lack of clear support for any particular model indicated model selection uncertainty; therefore, model averaging was employed for parameter estimation.

Overall, model-averaged apparent survival estimates revealed that males had lower survival than females and that reproductive individuals had lower survival than non-reproductive individuals (Fig. 1 shows estimates for a representative pair of sites; see ESM Fig. S1 for estimates for all sites). Model-averaged estimates showed large post-fire declines in apparent survival for both sexes and reproductive states in both the predator exclosures and controls (Fig. 1). Post-fire survival was not greatly impacted by food addition and still approached zero. During non-fire periods, food supplementation increased survival of rats of both sexes and reproductive conditions (Fig. 1). Apparent survival was greater in predator exclosures compared to controls regardless of burning, but this difference was marginal (Fig. 1; predator exclusion was associated with an average of 0.012 increased survival over a 13-week interval in non-fire periods and by an increase of 0.002 in post-fire periods).

Effects on reproductive transitions

Model-averaged estimates of Ψ showed that males both entered and remained in reproductive states at greater rates than females in all seasons (Fig. 2 shows estimates for a representative pair of sites; see ESM Fig. S2 for estimates for all sites). Most reproductive individuals of both sexes remained reproductive; this trend was slightly greater for males than females (Fig. 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-peaks in falls and winters without burns, and a separate 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 breeding seasons that did not distinguish between peak and non-peak breeding seasons (peak and non-peak with no distinguishing between burn and non-burn years; ESM, Table S2). Two-season breeding season models had no support (weight = 0.0) compared to three-season models (ESM, Table S2, model 7).

Model-averaged parameter estimates indicated that transitions to reproductive states (including rates of both non-reproductive individuals becoming reproductive and reproductive individuals remaining reproductive) were greatest during peak breeding seasons but that there was only a small drop in these transitions during non-peak/burn seasons (Fig. 2). However, transitions to reproductive states dropped considerably during non-peak/burn seasons (Fig. 2). Addition of food increased transitions to reproductive states while predator exclusion had a minimal effect on this parameter (Fig. 2).

Effects on abundance

The repeated measures ANOVA examining treatment effects on abundance indicated significant effects of feeding and fire treatments and their interaction ($P = 0.001$, <0.001, and 0.045, respectively). Examination of least square means showed that supplemental feeding increased abundances by 1.9 times while burning caused a threefold decline in abundance. Although the interaction of feeding and burning was significant ($P = 0.045$), there were still large declines in abundance in feeding areas following fires (2.9-fold decline). That these declines were nearly as large as post-fire declines in non-feeding areas suggests that the interaction of feeding and fire was not biologically meaningful. Predation and the interactions of predation with

Table 1 Model comparison table for multistate capture–mark–recapture analysis examining the effect of predation, supplemental feeding, and fire treatments on apparent survival (*S*) and transition probabilities (Ψ, probability of transition between reproductive and non-reproductive states) of hispid cotton rats (*Sigmodon hispidus*) in southwest Georgia, 2005–2009; capture probability was modeled as *p*(year + season) for all models

	Model	*K*	ΔQAICc	*ω*
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 includes number of parameters (*K*), model weights (*ω*, relative likelihood of a model in the set), and difference in Akaike's information criterion corrected for small sample size after quasilikelihood adjustment (ΔQAICc). Quasi-likelihood adjustments were made using an estimated $\hat{c}$ of 1.262. Bold text indicates treatment effects (all other effects are similar between models throughout the set). Only models with ΔQAICc < 4 are shown here (the top ranked 12 models of 55 in the overall set)

feeding and fire had no significant effect on abundance ($P > 0.1$).

Analyses of radio-telemetry data

A total of 279 cotton rats were collared during this study, of which 212 rats met criteria for survival analysis; of these, 29 were censored for at least some time during which they were not tracked (slipped/chewed off collar, or experienced transmitter failure), but were later recollared and reentered into the analysis, and 62 rats were censored and never reentered into analysis. Causes for censoring included slipping/chewing off collars ($n = 21$), emigrating from the 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, undetected emigration, or carrying off of the rat and/or collar by a far-ranging predator. For a discussion of the fates of censored rats, and a comparison with uncensored rats, see ESM, Appendix S3.

There was strong evidence for seasonal and fire effects on survival of collared rats (Table 2). Survival in spring, summer, and fall were similar (Table 2, models 8, 9, and 11; ΔAICc were all within two of each other) while survival during the winter where burning occurred and the winter 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, model 1; survival varying by season) indicated that winter survival in the non-burn year was greater than other seasons, whereas survival in the winter of the burn year was quite low (Fig. 3a).

There was poor support for supplemental feeding and predation treatment effects on collared rat survival; the highest ranked model with a food or predation term had moderate support (ΔAICc = 4.14; Table 2, model 3). This model indicated an interactive effect of season with the predator exclusion treatment. Parameter estimates from this model showed that survival of rats was similar between controls and exclosures for all seasons except the winter of

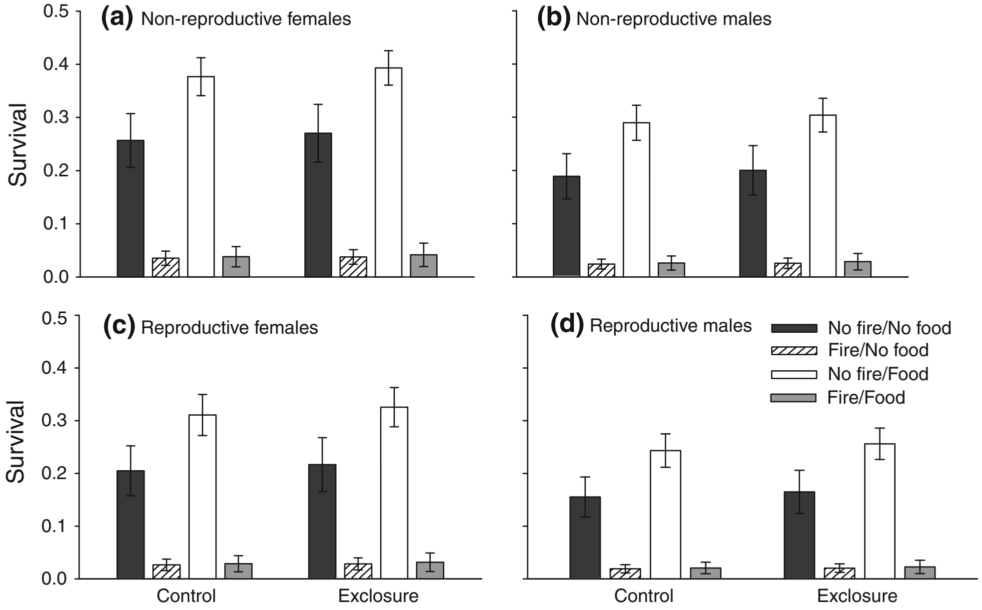

Fig. 1 Model-averaged estimates (±unconditional SE) of apparent survival of hispid cotton rats (*Sigmodon hispidus*) in southwestern Georgia between 2005 and 2009 in response to prescribed fire, supplemental feeding, and mammalian predator control treatments. Estimates are given for non-reproductive (**a**, **b**) and reproductive (**c**, **d**) females (**a**, **c**) and males (**b**, **d**). Estimates were generated using multistate capture–mark–recapture models. Survival is estimated over 13-week intervals. Estimates are given for representative sites: *Exclosure* indicates mammalian predator exclusion while *Control* indicates mammalian predator access. See Electronic Supplementary Materials Fig. S1 for estimates for all sites

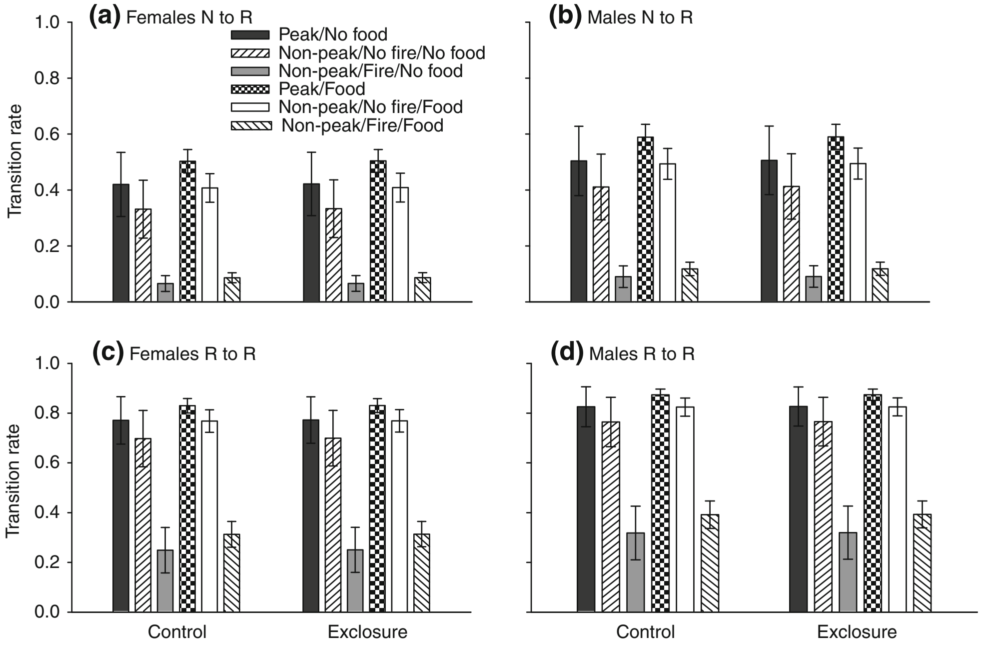

Fig. 2 Model-averaged estimates (±unconditional SE) of rates of reproductive transitions for male and female hispid cotton rats during peak breeding seasons (spring and summer), non-peak seasons during which burning did not occur, and non-peak seasons during which burning occurred, in southwestern Georgia between 2005 and 2009. Transitions include probability that non-reproductive individuals became reproductive (*N to R*; **a**, **b**), and reproductive individuals remained reproductive (*R to R*; **c**, **d**), conditional on survival. Estimates were generated from multistate capture–mark–recapture models and are given separately for females (**a**, **c**) and males (**b**, **d**). Transitions occurred over 13-week intervals. Estimates are given for representative sites: *Exclosure* indicates mammalian predator exclusion while *Control* indicates mammalian predator access. See Electronic Supplementary Materials Fig. S2 for estimates for all sites

Table 2 Factors influencing survival of radio-collared hispid cotton rats treated with supplemental feeding, prescribed fire, and mammalian predator exclusion in southwestern Georgia from June 2007 to August 2009

Model no.	Model	*K*	ΔAICc	ω
1	Season	5	0.00	0.57
2	Winter (burn)[a]	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)[b]	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

Survival was estimated and modeled using Cox proportional hazard models (Cox 1972). See Table 1 for column definitions. "|"indicates additive and interactive effects of the variables included. Single season models (i.e., *Spring* or *Fall*) modeled all other seasons with a constant survival while allowing that season's survival to vary. Models with a *season* effect (i.e., *Food|season*) allowed survival to vary for each season

[a] Winter (burn) refers to the winter of 2009 during which all sites were burned

[b] Winter (non-burn) refers to the winter of 2008 during which no sites were burned

the burn year, during which time survival was lower in predator exclosures than controls (Fig. 3b).

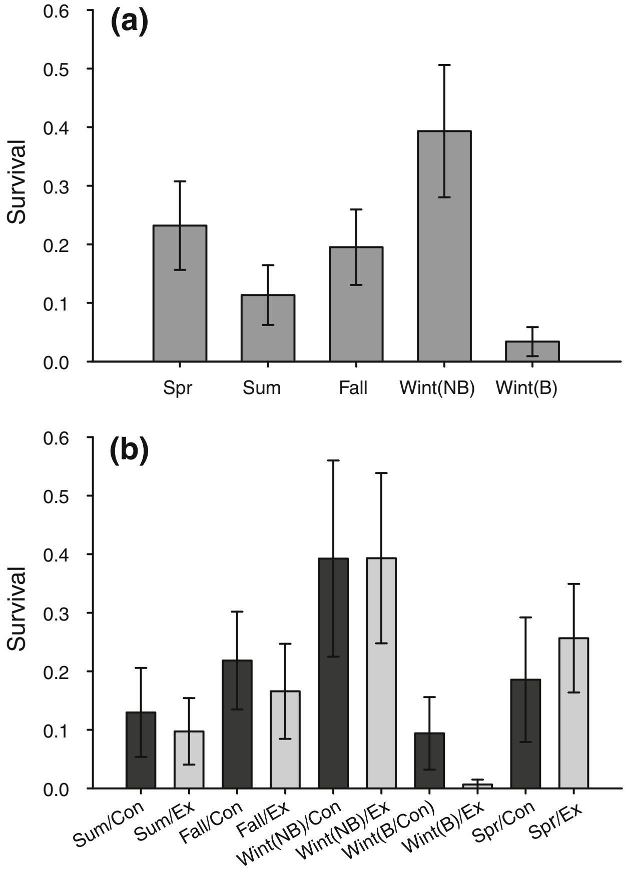

Fig. 3 Survival estimates (±SE) of radio-collared hispid cotton rats in southwestern Georgia between 2007 and 2009, generated using Cox proportional hazard models (Cox 1972). Estimates for (**a**) were generated using a model where survival varied by season (Table 2, model 1). Estimates for (**b**) were generated using a model where survival varied by season and predation treatment (Table 2, model 3). *Ex* indicates mammalian predator exclusion while *Con* indicates mammalian predator access. *Wint(B)* refers to winter 2009 during which all sites were burned. *Wint(NB)* refers to winter 2008 during which burns were not carried out

Fire effects on radio-collared rats

Thirty-four rats were tracked during the prescribed fire (11 non-feeding predator control, 8 non-feeding exclosure, 8 fed predator control, and 7 fed exclosure rats). All rats survived the fire by sheltering in burrows within their home ranges or in areas that did not burn completely. All rats either died or emigrated within 12 days of the fire. Of the 34 collared rats, 14 (41%) died due to predation, 8 (24%) emigrated to small, unburned patches within the larger burn area, and 10 (29%) emigrated to unburned areas completely outside the burn unit. Of the remaining two rats, one chewed its collar off in a hole in the burn area, while the other stayed within the burn area (an unfed predator exclosure) and died of starvation 7 days post-fire.

Of the eight rats that moved to unburned patches within the larger burn area, six moved less than 50 m. The unburned patch these six rats came to inhabit was already included in or within 50 m of the rats' pre-fire home ranges; it is likely that the rats were already familiar with the patch they invaded. These six rats were captured during the next trapping period; five had lost body mass during the interval. The mean percent mass change was −14.0% over 33 days. To determine if this was an artifact of the winter season, body mass changes of collared rats over the 2008 winter were also calculated. Of nine collared rats which were captured in both winter 2008 sessions (35 days between sessions), the mean body mass change was a gain of 11.0%. A *t* test indicated that body mass changes over the period between the first and second winter sampling periods differed significantly ($P < 0.001$, $t_{13} = 4.44$) between the winters of 2008 and 2009.

The two other rats that moved to unburned areas in the larger burn unit made moves of approximately 175–275 m. It is unlikely that these rats were previously familiar with these patches. Of the ten rats that emigrated to areas outside of the burn unit, all did so in a single night and moved distances of 50–700 m. Only one moved to the nearest unburned area.

Discussion

Fire effects

Of the three treatments experimentally applied to cotton rat populations in this study, prescribed fire had the largest impact. Burning caused precipitous declines in survival, abundance, and rates of transitions to reproductive states (including rates of non-reproductive individuals becoming reproductive and of reproductive individuals remaining reproductive) regardless of the presence of supplemental food or absence of mammalian predators. Observations of radio-collared rats support the hypothesis that cotton rat declines following fires were due primarily to non-mammalian 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 others that remained in small, unburned patches in the overall burn unit lost body mass. This suggests that the loss of herbaceous food sources by burning negatively affected 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; in this study, 76% of all collared rat deaths) and cotton rat populations experience near-complete turnover in as little as 5–8 months (Goertz 1964).

These results suggest that, in ecosystems where fires are frequent, cotton rat populations are heavily influenced by fires. Similar sharp post-fire declines in cotton rat abundances have been observed in native tallgrass prairies, sacaton grasslands, and other southern pine forests (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 2 years following spring burns but declined 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 sources and reduce litter which may inhibit movement through vegetation.

Similar results have been observed with other diurnal rodents. An experiment involving supplemental feeding and cover removal (by mowing; Perrin and Johnson 1999) found that while striped mouse (*Rhabdomys pumilio*) abundance increased in areas with both feeding and cover, no mice lived in mowed areas, even when supplemental food was provided. These observations suggest that, among diurnal prey species, which are especially vulnerable to visual predators, predation risk is likely to supersede food resource availability in importance. However, this may not be true in all systems. A study on wildfires in Alaska found that voles did not consistently recolonize burned areas until berry production approached pre-burn levels (West 1982).

It should be noted that, although this study considered CMR data over three burn cycles and telemetry data over one burn cycle, during burn years, all sites were burned. As such, there was no fire control; fire effects were assessed by comparing trends between burn years and non-burn years. This leaves untested the possibility that cotton rat populations in our study site simply exhibited periodic fluctuations characterized by biannual winter crashes in abundance and declines in survival and reproductive transitions and would do so even in the absence of fire. However, this seems unlikely given the immediate fire response observed with radio-collared rats during the 2009 burn. If any of the observed effects are likely to have been an artifact of the experimental design, it is most likely to be the observations regarding body mass changes of collared rats between the winter trapping periods in 2008 (a non-burn winter) and 2009 (a burn winter) because we were unable to monitor collared rats through additional burn cycles.

Predation and supplemental feeding effects

Unlike similar studies which have observed interactive effects of predation and supplemental feeding on mammal populations (Tiatt and Krebs 1983; Desy and Batzli 1989; Hubbs and Boonstra 1997), our study detected no interactive effects on cotton rat populations or any strong effects of mammalian predator removal at all. The lack of mammalian predation effects may seem counterintuitive 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, either as a single treatment or in conjunction with feeding. Previous studies examining effects of predator manipulation on cotton rats (Wiegert 1972; Guthery and Beasom 1977) suggest that the effects of such treatments vary according to the predators manipulated. Guthery and Beasom (1977) removed only mammalian predators from areas where cotton rats occurred, and detected no change in survival or density. Wiegert (1972) excluded all predators from a study area and subsequently allowed access to avian predators while continuing to exclude mammalian predators. Wiegert (1972) determined that avian predators had a greater impact on cotton rat populations than mammalian predators and concluded that, although mammalian predators kill some cotton rats, they are an incidental cotton rat predator. These results are consistent with our own which suggest that snakes and raptors killed cotton rats that would have otherwise been killed by mammalian predators. Alternatively, it is possible that food resources, rather than predation, limit 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 the CMR analyses did not support a strong predation treatment effect on apparent survival, 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 exclosures). This may indicate a sub-lethal predation effect, but we believe it to be due instead to site effects. Specifically, one section of the unfed predator control containing collared rats did not burn completely. Six collared rats had home ranges adjacent to this area and moved into it following the fire. This area (measuring $\sim 1{,}350\ \mathrm{m}^2$) provided cover, and as a result, it is likely these rats were less vulnerable to predation. Given that these six rats made up a significant portion of rats in predator control treatments during the burn ($n = 18$), this may have skewed the results relating to post-fire predation treatment effects on collared rat survival. If the burn in this area had been more complete, 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 suggest that negative short-term fire effects can be mitigated if unburned refugia remain (although rats seemed unable to reliably find such refugia at distances greater than ~50 m from their home ranges).

With respect to the supplemental feeding treatment, there was an interesting relationship between feeding effects and survival of reproductive rats. Feeding was associated with both increased survival and rates of transition to reproductive states, but survival was lower among reproductive rats than non-reproductive rats. This relationship is somewhat contradictory and could occur by two means. The increase in survival associated with feeding could be disproportionately carried by non-reproductive individuals (i.e., if feeding increased survival in both reproductive and non-reproductive rats, but the increase was proportionally greater among non-reproductive than reproductive rats). Alternatively, the increased rate of transition to reproductive states could be disproportionately made up of non-reproductive individuals becoming reproductive. A close look at the results shows that both situations occur, although neither was very dramatic (Figs. 1 and 2; S1 and S2). Some interesting conclusions can be drawn from these observations. Since the rate of reproductive rats remaining reproductive was already high in non-feeding areas (Fig. 2 and S2), there may simply have been less potential for this rate to increase further. Non-reproductive rats may use extra resources provided by feeding towards body growth. Non-reproductive cotton rats are likely to be younger rats and reproductive maturity is achieved at a given body size (50 g) regardless of the time it takes to reach that size (Bergstrom and Rose 2004). Rats that are already reproductive may use supplemental food in other ways. A previous study on effects of supplemental feeding on cotton rats found that feeding increased the number and mass of newborns (Campbell and Slade 1995). It is possible that our treatments affected reproductive parameters such as these, but we did not have the data for such an assessment.

It is also worth considering why the CMR analysis showed support for increased apparent survival in feeding areas while no such effect was detected among collared rats. There are two possible explanations. First, the CMR analysis included individuals of all ages while collared rats were by necessity older and larger animals (to be big enough to carry collars). It is possible that food resources were less influential on survival of older/larger rats than the overall population. This could occur if large rats occupied more ideal habitats with more reliable food sources than smaller rats. Indeed, there is evidence that large cotton rats maintain home ranges in more ideal habitats while smaller rats are marginalized to poorer habitats, especially when densities are high (Goertz 1964). Such a situation could also explain the observation above that survival of reproductive rats (which are likely to be larger and older rats) increased to a lesser degree than non-reproductive rats in feeding plots. Alternatively, this effect may be due to the confounding of survival and permanent emigration in CMR analyses. In CMR analyses, if a marked animal is not recaptured, it may have either died or permanently emigrated. Therefore, changes in survival may be confounded with changes in emigration rates. A previous study examining the effects of supplemental feeding on cotton rats found that cotton rats in feeding areas decreased long-term movements, probably by decreasing home range shifts over time (Sulok et al. 2004). Home range shifts could appear as permanent emigration if a shift moved a rat away from the trapping grid. If feeding decreased home range shifting in our study, the increased apparent survival in feeding grids could reflect decreased emigration rates rather than changes in actual survival.

Conclusions

Our results suggest that cotton rat population dynamics in our study site were primarily driven by fire events. Population responses following fires appeared to be strongly influenced by fire-caused loss of cover and associated increases in non-mammalian predation. Population-level effects relating to mammalian predation did not appear to be strong. Food was also important to cotton rats, and caused increases in all of the demographic parameters considered here. Although there was evidence that rats remaining in burned areas were negatively affected by changes in food resource availability, food effects were overwhelmed by predation effects following fires.

Acknowledgments We thank the Joseph W. Jones Ecological Research Center and the University of Florida for providing funding, manpower, and equipment. We thank the many technicians who assisted with data collection, entry, and proofing. For executing burns, we thank J. Atkinson, S. Smith, C. Eddins, and B. Williamson. J. Brock and M. Simmons assisted with GIS and database management, respectively. Thanks to B. Bass for providing burn evaluation data. Special thanks to J. Rutledge for assistance with fieldwork, logistics, and more. We also thank P. Banks and two anonymous reviewers for comments on an earlier version of this manuscript. Our study complies with the current laws of the USA.

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