

The influence of mammalian predator exclusion, food supplementation, and prescribed fire on survival of *Glaucomys volans*

BINAB KARMACHARYA, JEFFREY A. HOSTETLER, L. MIKE CONNER,* GAIL MORRIS, AND MADAN K. OLI

Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, P.O. Box 110430, Gainesville, FL 32611-0430, USA (BK, MKO)

Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20013-7012, USA (JAH)

Joseph W. Jones Ecological Research Center, 3988 Jones Center Drive, Newton, GA 39870, USA (LMC, GM)

* Correspondent: mconner@jonesctr.org

Little is known about demographic parameters of the southern flying squirrel (*Glaucomys volans*) or the factors influencing those parameters. We conducted capture–mark–recapture studies from January 2005 to September 2009, and from May to November 2010 to provide rigorous estimates of survival rates for the southern flying squirrel in a longleaf pine ecosystem. We also examined the effect of experimental food supplementation, prescribed fire, and mammalian predator exclusion on survival rates. Monthly apparent survival rates estimated from the 2 studies were 0.85 ± 0.01 SE and 0.81 ± 0.04 , respectively. Prescribed fire positively influenced survival; survival increased for a period up to 9 months after burns. Evidence that food supplementation and mammalian predator exclusion substantially affected survival rates was weak. These results suggest that the southern flying squirrel population in our study site during the study period was not food-limited, and that mortality due to mammalian predators is insubstantial. However, we do not know if any reduction in mortality due to mammalian predator exclusion could have been compensated for by an increase in mortality due to predation by raptors and snakes.

Key words: arboreal small mammal, capture–mark–recapture (CMR), capture probability, demography, *Glaucomys volans*, mammalian predator exclusion, prescribed fire, supplemental food, survival rate

© 2013 American Society of Mammalogists

DOI: 10.1644/12-MAMM-A-071.1

Food and predation are 2 of the most important factors influencing population dynamics of small mammals; every small mammal requires food to survive and is a potential prey for others. Studies that have evaluated population-level influences of experimentally supplemented food have revealed that food supplementation can lead to a larger body size (Cole and Batzli 1978), longer breeding season (Hansen and Batzli 1979; Taitt and Krebs 1983), higher density (Hubbs and Boonstra 1997), increased survival (Ransome and Sullivan 2004), and larger litter size (Campbell and Slade 1995; Cole and Batzli 1978). However, the population-level effects of food supplementation can vary among species and habitats. For example, recent studies in a longleaf pine (*Pinus palustris*)–wiregrass (*Aristida beyrichiana*) ecosystem showed that food supplementation increased survival, abundance, and rate of transition from nonreproductive to reproductive states of hispid cotton rats (*Sigmodon hispidus*—Morris et al. 2011b); on the same site, supplemental food increased abundance but not survival of cotton mice (*Peromyscus gossypinus*) and oldfield

mice (*P. polionotus*—Morris et al. 2011a). Likewise, supplemental food increased population size but had no influence on proportion of adults breeding, survival, or recruitment rates of northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*—Ransome and Sullivan 1997). However, Ransome and Sullivan (2004) reported that food supplementation increased survival of northern flying squirrels but had no effect on red squirrels.

Predation plays a vital role in the population dynamics of any prey species. An increase in mortality rate is the most obvious effect of predation. Predator exclusion or removal experiments have yielded increased densities of cotton rats (Schnell 1968) and increased survival of degus (*Octodon degus*—Meserve et al. 1993). In southern Georgia, experimental exclusion of mammalian predators had no effect on



demographic parameters of hispid cotton rats and cotton mice, but it positively influenced survival and abundance of oldfield mice (Morris et al. 2011a, 2011b).

In small mammal species inhabiting fire-maintained ecosystems, such as the longleaf pine ecosystem, frequency and scale of fire can also influence population parameters (Pyne et al. 1996). Fire reduced survival, abundance, or transition from nonreproductive to reproductive states, or a combination of these factors, in cotton rats, cotton mice, and oldfield mice (Morris et al. 2011a, 2011b); similar results were reported for northern flying squirrels in ponderosa pine (*Pinus ponderosa*) and mixed conifer forests (Lehmkuhl et al. 2006). Tree squirrels appeared to benefit indirectly from low-intensity ground fires, which stimulated cone and fungi production, and created open stands that facilitate foraging (Weigl et al. 1989).

Several studies have experimentally evaluated effects of food, predation, and fire on demographic variables of small mammals (Krebs et al. 1995; McNamara and Houston 1987; Morris et al. 2011a, 2011b; Sinclair and Pech 1996). However, we know of no study that has tested the population-level effects of food, fire, and predation on the southern flying squirrel (*Glaucomys volans*). In fact, little is known about demography and population dynamics of the southern flying squirrel, the most widely distributed flying squirrel of North America. Thus, our specific objectives were to provide rigorous estimates of survival rates, and to test for sex-specific and seasonal variation in survival; and to experimentally test for effects of food supplementation, mammalian predator exclusion, and prescribed fire on survival of the southern flying squirrel. However, we acknowledge that exclusion of mammalian predators may not have a substantial effect on the survival of these cavity-dwelling arboreal mammals, because raptor and snakes generally are more important predators than are mammalian mesocarnivores (Carey et al. 1992; Laves and Loeb 1999; Mitchell et al. 1999; Rudolph et al. 1990). It was not logistically feasible to exclude avian and snake predators.

MATERIALS AND METHODS

Study area.—The study was conducted at the Joseph W. Jones Ecological Research Center (hereafter, the Center) at Ichauway, a 12,000-ha site managed for research, education, and conservation, located in Baker County, Georgia. The site is primarily a longleaf pine and wiregrass ecosystem with associated hardwood tree species, wetlands, slash pine (*Pinus elliotii*), and a variety of other habitats (Atkinson et al. 1996). This ecosystem is shaped by frequent fire, induced by either humans or lightning (Van Lear et al. 2005). Our study site was managed by prescribed fire (Glitzenstein et al. 1995), and the Center employed both dormant and growing season burns in an approximate 2-year burn rotation.

Study species.—The southern flying squirrel is 1 of 2 species of the genus *Glaucomys*. Its distribution ranges from temperate

to subtropical pine-hardwood forests from southernmost Quebec, Canada, southward through the eastern one-half of the United States to Honduras (Dolan and Carter 1977). Southern flying squirrels are relatively long lived (~10 years), and use tree cavities for nut storage, latrines, den sites, and breeding sites; individuals may use several cavities (Brady et al. 2000) and a single cavity is used by several individuals (Layne and Raymond 1994). They compete with other cavity-nesting species, such as the red cockaded woodpecker (*Picoides borealis*), for available nest sites (Borgo et al. 2010; Stabb et al. 1989). It is generally accepted that populations of southern flying squirrels have increased and that they are a threat for conservation of endangered red cockaded woodpeckers (Borgo et al. 2010; Werner and Peacor 2003), but little is known about the population ecology of this species.

Field methods.—There were 4 mammalian predator exclusion plots in the Center; each was surrounded by 1.21-m-tall woven-wire fencing with 3 parallel electric wires at the top, middle, and bottom to prevent entry of mammalian predators by climbing and digging. The size of the fence weave allowed movement of small mammals and snakes in and out of the predator enclosure. Significantly fewer mammalian predators in enclosure plots than in control plots was evident from regular track counts and thermal camera surveys (Conner et al. 2010). When mammalian predators were detected inside enclosures, efforts were made to trap and remove them. A nearby plot of the same size and with similar habitat was selected as a control plot for each enclosure. Therefore, there were 4 enclosure and 4 control plots. These control and enclosure plots ranged from 36 to 49 ha in size. Because of their geographical proximity and habitat similarity, pairs of control and enclosure plots were considered as 1 site.

As part of an ongoing small mammal study, a 12 × 12 trapping grid with 15 m between stations was established in each control and enclosure plot. One Sherman live trap (H. B. Sherman Traps, Inc., Tallahassee, Florida) was placed on the ground at each station. Additionally, 24 traps (4 traps in each alternate row) were set at about 2 m high on the nearest suitable tree. Grids in each plot were trapped once per season from January 2005 through June 2007, and twice per season from July 2007 through September 2009. Prescribed fires were executed in February of 2005, 2007, and 2009 according to the Center's burn plan in all the study plots.

In May 2010, 6 plots (2 randomly selected controls and all predator enclosures) were chosen for a 2nd flying squirrel study. Traps, mounted on wooden platforms, were set 2 m high on the nearest suitable tree in the same 12 × 12 small mammal trapping grid at each station. Trapping was done twice every season from May through November 2010. Supplemental food was provided in 2 randomly selected enclosures from July 2010 to October 2010. Plastic feeders with 300 g of rolled oats were placed 2 m high up on trees in 4 × 4 grids with approximately 60 m between the stations. Feeding stations were checked and refilled every week. Motion-sensitive trail cameras revealed the regular use of feeding stations by flying squirrels and other small mammal species.

During each trapping session, traps were set for 4 consecutive nights (Monday–Thursday). Traps were baited with rolled oats and mixed bird feed, and checked every morning. Fire ant invasion of baited traps for small mammals is a major problem in the southeastern United States (Mitchell et al. 1996), so we sprinkled a granular insecticide (Talstar Nursery Granular Insecticide, FMC Corporation, Philadelphia, Pennsylvania) around each trap on the ground to prevent fire ant infestation. Newly caught individuals were marked with metal ear tags in both ears and released at the capture site. For all captured individuals we recorded date, location, identity (if previously captured), sex, mass, state (adult or juvenile based on mass), reproductive condition, and hind-foot length.

All field methods were approved by the University of Florida Institute of Food and Agricultural Sciences Animal Research Committee and were in accordance with the recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Statistical methods and capture–mark–recapture analysis.—Models were built for program MARK version 6.1 (White and Burnham 1999) by analyzing capture–mark–recapture data with R (version 2.12.1—R Development Core Team 2010) package RMark 2.0.1 (Laake and Rexstad 2009). Monthly apparent survival (ϕ) and capture probability (p) were estimated and modeled using Cormack–Jolly–Seber models. We performed a goodness-of-fit test using the median \hat{c} approach in program MARK (White and Burnham 1999) and found no evidence of overdispersion or lack of fit ($\hat{c} = 1.00$). Akaike's information criterion corrected for small sample size (AIC_c) was used for model comparison and statistical inferences (Burnham and Anderson 2002). Using this approach, models with a difference in AIC_c (ΔAIC_c) of < 2 are considered to have similar support with no evidence for difference among models being compared; $2 \leq \Delta AIC_c \leq 4$ suggests evidence for considerable difference, $4 \leq \Delta AIC_c \leq 7$ suggests substantial evidence for difference, and $\Delta AIC_c > 7$ is generally indicative of overwhelming evidence for substantial difference in support received by the models being compared (Burnham and Anderson 2002). The model with the lowest AIC_c value is considered the most parsimonious. In some of our analyses, no single model received overwhelming support, suggesting model selection uncertainty; we used model averaging to address this issue (Burnham and Anderson 2002).

There were twenty-seven 4-day capture occasions from January 2005 to September 2009, and five 4-day capture occasions from May to October 2010. Each year was divided into 4 seasons; spring (20 March–20 June), summer (21 June–22 September), fall (23 September–20 December), and winter (21 December–19 March). Because control and enclosure plots within each site shared similar habitat characteristics, we also tested for a site effect on capture probability and apparent survival rate. Time intervals between sampling occasions varied (most were 2 or 4 months); time intervals between sampling occasions (number of months) were supplied to

program MARK such that the program provided estimates of monthly apparent survival probabilities.

Capture–mark–recapture data were collected from January 2005 to September 2009 (study designed for terrestrial and semiarboreal small mammals), and from May to October 2010 (study designed for the arboreal flying squirrel); these data sets were analyzed separately because they were collected using somewhat different study designs. The 1st, longer-term data set was used to estimate the apparent survival rate and to test for the effects of prescribed fire and mammalian predator exclusion on survival. The 2nd, shorter-term data set was used primarily to test the effect of food supplementation on survival.

We conducted preliminary analyses to identify the best base model for the capture probability (p) and apparent survival probability (ϕ) such that treatment effects could be evaluated in subsequent analyses. The best base model for p was investigated with time-dependent ϕ , taking into account the potential influence of trapping session, year, sex, season, site, and their additive and interactive effects on capture probability. The best-supported model for p was then used to investigate the best base model for ϕ taking into account the potential influence of trapping session, year, sex, season, site, and their additive and interactive effects on survival. Effects of predator exclusion and prescribed fire on ϕ were then added to the best base model of the 1st data set; likewise, the effect of predator exclusion and food supplementation was added to best base model for the 2nd data set.

The effect of prescribed fire on small mammals is mediated primarily through changes in habitat brought about by the fire event (Smith 2000). Duration of this effect can vary for different species (Morris et al. 2011a, 2011b). Thus, we tested for different effect windows of prescribed fire for southern flying squirrel by fixing the survival for all sessions but those following fire and allowing survival to vary for different lengths of time (3, 6, and 9 months) after the fire event. We did not examine the treatment effect beyond 9 months to avoid the potentially confounding effect of annual variation on survival rate. The best-supported fire effect window on survival was then added to the base model to test for the effect of fire on flying squirrel survival. Unless indicated otherwise, all means are presented $\pm 1 SE$.

RESULTS

From January 2005 to September 2009, we captured 281 individual flying squirrels 556 times. Base model analysis revealed that capture probability was best described by an additive effect of sex and season (Table 1a). Overall capture probability was 0.30 ± 0.03 , but it was substantially higher for females (0.40 ± 0.05) than for males (0.18 ± 0.04).

The most-parsimonious model for monthly apparent survival rate included an additive effect of site and year (Table 1b). The overall monthly apparent survival was 0.85 ± 0.01 , but it varied over years and sites (Fig. 1). Overall monthly survival was lowest (0.68 ± 0.07) in 2007 and highest (0.94 ± 0.03) in 2009; likewise, survival varied among sites, ranging from 0.79

TABLE 1.—Model comparison table for Cormack–Jolly–Seber capture–mark–recapture analysis to investigate the best base model for a) capture probability (p), and b) survival (ϕ) for southern flying squirrels at the Jones Ecological Research Center, Newton, Georgia, from 2003 to 2009. The table includes the number of parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and model weights (relative likelihood of models in the set). Only the 5 best-supported models are presented.

Model	K	AIC_c	ΔAIC_c	Model weight
a) Capture probability				
p (sex + season)	31	606.009	0.000	0.884
p (site + sex)	31	612.478	6.469	0.035
p (sex * season)	34	612.537	6.528	0.034
p (sex + year)	32	613.415	7.406	0.022
p (sex)	28	613.773	7.764	0.018
b) Survival rate				
ϕ (site + year)	13	575.610	0.000	0.583
ϕ (sex + year)	11	577.366	1.757	0.242
ϕ (year)	10	578.080	2.470	0.170
ϕ (sex + site)	10	587.248	11.639	0.002
ϕ (site)	9	587.791	12.181	0.001

± 0.04 in site 1, to 0.88 ± 0.01 in site 2. The 2nd most-parsimonious model (which differed from the top model by $\Delta AIC_c = 1.75$) included an additive effect of sex and year, with higher monthly survival for males than for females (Table 1b; Fig. 2). The top 3 models for ϕ differed by $\Delta AIC_c < 3$, indicating model selection uncertainty; thus, we used model averaging to obtain model-averaged survival estimates. Model-averaged survival was highest (0.957 ± 0.031) for males at site

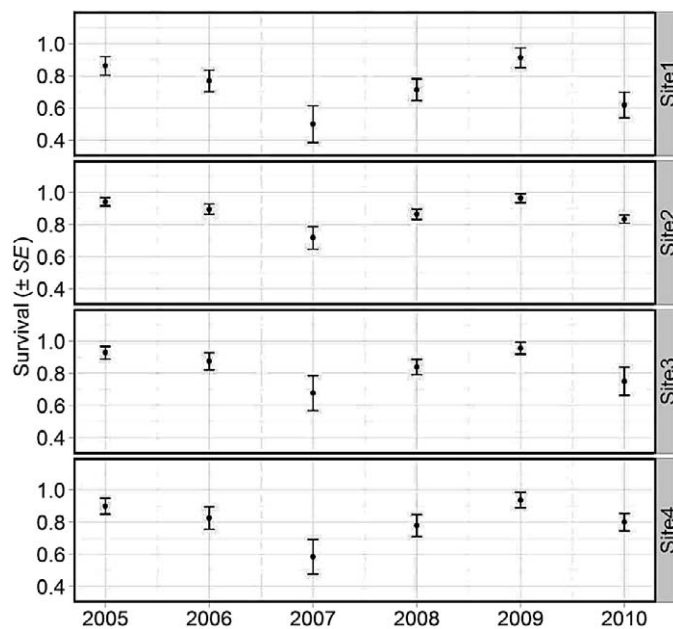


FIG. 1.—Monthly apparent survival estimates ($\pm SE$) of southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia, at 4 sites from 2005 to 2010. The estimates of survival for years 2005–2009 were modeled as ϕ (site + year; Table 1b) and for the year 2010 as ϕ (site; Table 3b).

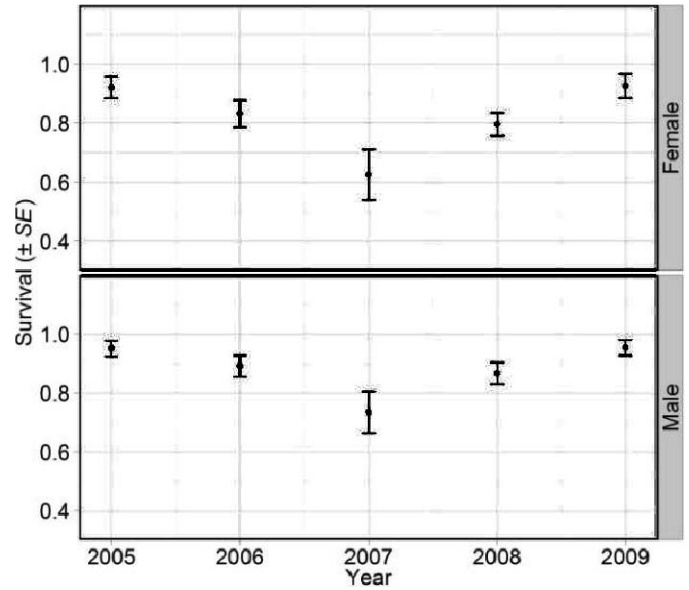


FIG. 2.—Monthly apparent survival estimates ($\pm SE$) of male and female southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia, from 2005 to 2009. The estimates of survival were modeled as ϕ (sex + year; Table 1b).

2 in 2009 and lowest (0.561 ± 0.127) for females at site 1 in 2007 (Appendix I).

Analyses to determine the duration of fire effect on survival did not reveal strong support for any particular effect window (Table 2a). There was some evidence ($\Delta AIC_c = 2.62$) that prescribed fire positively influenced survival rates (Table 2a), with higher monthly survival following burns (Fig. 3; fire effect coefficient = 2.23, 95% confidence interval: -0.50 –

TABLE 2.—Model comparison table for Cormack–Jolly–Seber capture–mark–recapture analysis of southern flying squirrels to investigate the effects of a) prescribed fire and b) mammalian predator exclusion on survival (ϕ) at the Jones Ecological Research Center, Newton, Georgia, from 2003 to 2009. The best base model for ϕ was an additive effect of site and year, and the treatment effects are indicated by boldface text. For this analysis capture probability (p) was modeled as p (sex + season). Only the 5 best-supported models are presented. See Table 1 for column definitions.

Model	K	AIC_c	ΔAIC_c	Model weight
a) Effect of prescribed fire				
ϕ (site + year + fire effect up to 6 months)	14	572.984	0.000	0.447
ϕ (site + year + fire effect up to 9 months)	14	573.285	0.301	0.384
ϕ (site + year)	13	575.610	2.626	0.120
ϕ (site + year + fire effect up to 3 months)	14	577.403	4.419	0.049
b) Effect of mammalian predator exclusion				
ϕ (site + year)	13	575.610	0.000	0.605
ϕ (site + year + predator exclusion)	14	576.464	0.855	0.395

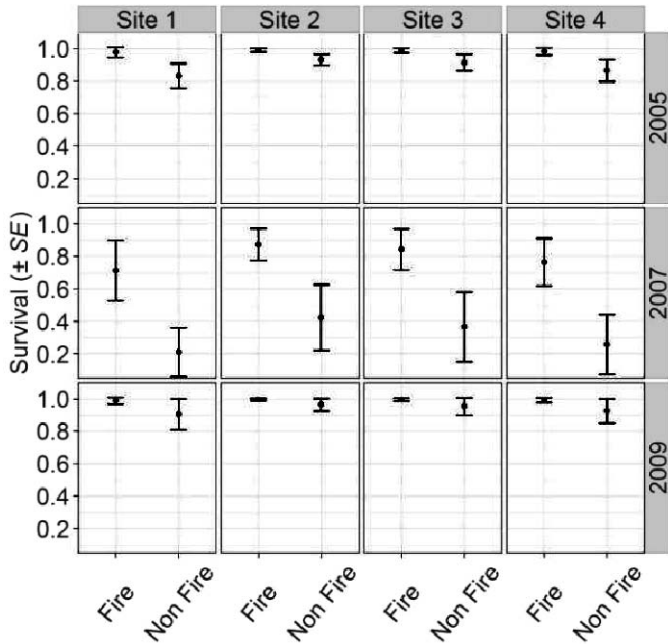


FIG. 3.—Monthly apparent survival estimates ($\pm SE$) of southern flying squirrels with and without the effect of prescribed fire at 4 sites in the Jones Ecological Research Center, Newton, Georgia, through 3 prescribed fire cycles (with burns in 2005, 2007, and 2009). The effect of prescribed fire on survival was modeled as ϕ (site + year + fire effect; Table 2a).

4.96). Model-averaged estimates also revealed improved survival rates postfire up to a period of 9 months following all 3 burns at all 4 sites (Appendix II).

Models with and without the effect of mammalian predator exclusion received similar support, suggesting no substantial effect of mammalian predators on southern flying squirrel survival (Table 2b). Both single-model (Fig. 4) and model-averaged estimates (Appendix III) revealed similar monthly apparent survival for control and mammalian predator exclusion sites.

During the May–November 2010 capture–mark–recapture study, we captured 187 individual flying squirrels 702 times. Base model analysis revealed that capture probability was best described by an additive effect of sex and site (Table 3a). Overall capture probability was 0.69 ± 0.03 , but it was substantially higher for females (0.81 ± 0.04) than for males (0.56 ± 0.05).

Base model analysis revealed that the monthly apparent survival rate was best described by a site-specific survival model (Table 3b). Overall monthly apparent survival was 0.81 ± 0.01 ; it was the highest (0.83 ± 0.03) at site 2 and lowest (0.62 ± 0.08) at site 1 (Fig. 1). Model-averaged estimates revealed that monthly site-specific apparent survival was the highest for males at site 2 (0.83 ± 0.03) and lowest for females at site 1 (0.68 ± 0.12 ; Appendix IV).

Models with and without an additive effect of food supplementation received similar support, providing no evidence that supplemental food substantially affected

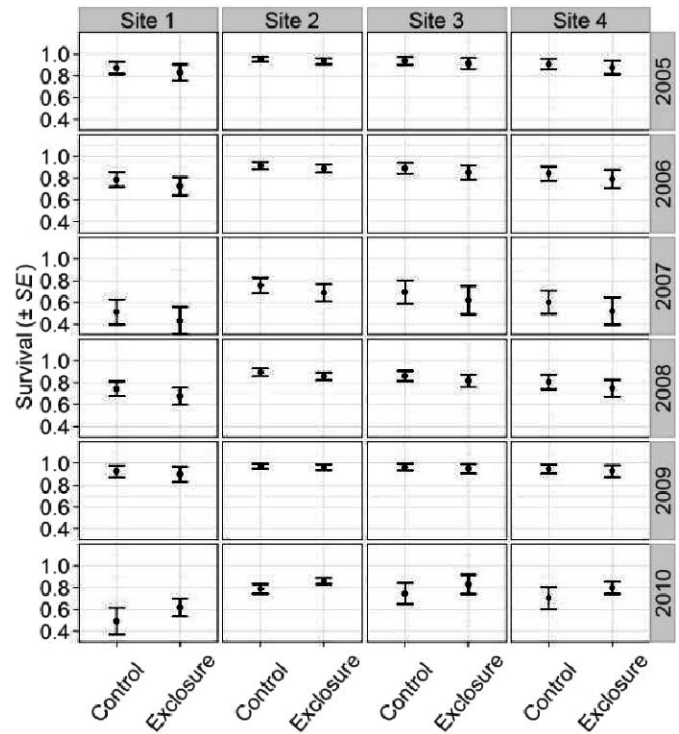


FIG. 4.—Monthly apparent survival estimates ($\pm SE$) of southern flying squirrels at control and mammalian predator exclusion sites in the Jones Ecological Research Center, Newton, Georgia, at 4 sites from 2005 to 2010. The effect of predator exclusion on survival for the years 2005–2009 was modeled as ϕ (site + year + predator exclusion; Table 2b) and for the year 2010 as ϕ (site + predator exclusion; Table 4b).

survival (Table 4a). Both single-model estimates (Fig. 5) and model-averaged estimates (Appendix V) showed similar monthly apparent survival for control and food-supplemented sites.

TABLE 3.—Model comparison table for Cormack–Jolly–Seber capture–mark–recapture analysis to investigate a) the best base model for capture probability (p) and b) survival (ϕ) for southern flying squirrels at the Jones Ecological Research Center, Newton, Georgia, in the year 2010. Only the 5 best-supported models are presented. See Table 1 for column definitions.

Model	K	AIC_c	ΔAIC_c	Model weight
a) Capture probability				
p (sex + site)	9	594.350	0.000	0.495
p (sex + time)	9	595.151	0.801	0.332
p (sex)	6	597.322	2.972	0.112
p (sex * site)	12	599.515	5.165	0.037
p (sex * time)	12	600.540	6.189	0.022
b) Survival rate				
ϕ (site)	9	600.621	0.000	0.455
ϕ (constant)	6	601.720	1.099	0.263
ϕ (sex + site)	10	602.540	1.919	0.174
ϕ (sex)	7	603.675	3.054	0.099
ϕ (sex * site)	13	608.342	7.721	0.010

TABLE 4.—Model comparison table for Cormack–Jolly–Seber capture–mark–recapture analysis of southern flying squirrels to investigate the effects of a) food supplementation and b) mammalian predator exclusion on survival (ϕ) at the Jones Ecological Research Center, Newton, Georgia, in the year 2010. The best base model for ϕ was site-specific survival, and the treatment effects are indicated by boldface text. For this analysis capture probability (p) was modeled as p (sex + site). See Table 1 for column definitions.

Model	K	AIC_c	ΔAIC_c	Model weight
a) Effect of food supplementation				
ϕ (site)	10	600.621	0.000	0.634
ϕ (site + supplemental food)	11	601.717	1.096	0.366
b) Effect of mammalian predator exclusion				
ϕ (site + predator exclusion)	10	600.528	0.000	0.512
ϕ (site)	9	600.621	0.093	0.488

The most-parsimonious model testing for the effect of mammalian predator exclusion included an additive effect of predator exclusion (Table 4b). However, this model differed from the base model only by $\Delta AIC_c = 0.09$, suggesting that models with and without mammalian predator exclusion effect received very similar support. Monthly apparent survival did not substantially differ between control and mammalian predator exclusion sites (Fig. 4); model-averaged estimates of survival likewise revealed no detectable effect of mammalian predator exclusion on survival (Appendix III).

DISCUSSION

Despite its wide geographic distribution (Dolan and Carter 1977), little is known about the population ecology of the southern flying squirrel. In fact, we were unable to find any study that reported survival or population growth rate for this species; this is surprising given that it is an abundant species that is considered a pest in some areas (Borgo et al. 2010; Laves and Loeb 1999). Using a capture–mark–recapture approach, our study was undertaken to fill the gap in knowledge by providing estimates of survival rates. Furthermore, we experimentally tested for the effects of food, fire, and mammalian predation (arguably, 3 of the most important factors affecting small mammal demography) on survival of southern flying squirrels.

Capture probability was substantially higher during the 2nd study period when all the traps were set 2 m high in the trees, due perhaps to a greater density of tree traps, which increases accessibility for this arboreal species. These results are consistent with findings of earlier studies showing a higher trapping success for arboreal and semiarboreal species when traps are set up in trees (Gentry et al. 1968; Sawyer and Rose 1985). This reemphasizes the importance of appropriate trapping protocols for collecting reliable information on small mammal population dynamics (Risch and Brady 1996). Lehmkuhl et al. (2006), in a study using both tree and ground traps, reported a capture probability of 0.14 for northern flying squirrels, which is substantially lower than our estimates for southern flying squirrels. We found that females were more

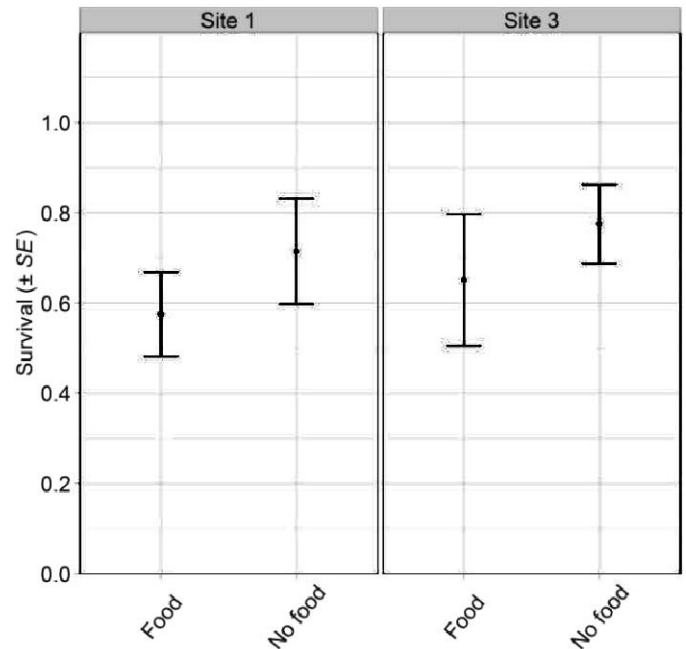


FIG. 5.—Monthly apparent survival estimates ($\pm SE$) of southern flying squirrels at sites with and without food supplementation in the Jones Ecological Research Center, Newton, Georgia, in 2010. The effect of food on survival was modeled as ϕ (site + supplemental food) (Table 4a).

likely to be captured than males, an observation also reported for the Siberian flying squirrel (*Pteromys volans*—Lampila et al. 2009). High energy requirements of females during pregnancy and lactation could make food more attractive to females, resulting in higher capture probabilities for females in baited traps.

Estimates of monthly apparent survival rates obtained from the 2 studies (i.e., using data collected during 2005–2009 and May–October 2010) yielded similar estimates of monthly apparent survival. Survival rates were slightly higher for males in both studies, due perhaps to sex-specific differences in predation risk. Site-specific variation in survival rate was consistent in both studies. These variations may reflect the influence of microhabitat differences among sites, or environmental variation, or both. Apparent annual survival for a close relative, the northern flying squirrel, has been reported to be 0.47–0.51 in eastern Washington State’s Cascade Range (Lehmkuhl et al. 2006), and 0.32–0.68 in the northern coastal range of Oregon (Gomez et al. 2005). Likewise, average annual adult survival for Siberian flying squirrels has been reported to be 0.43–0.53 (Lampila et al. 2009). The overall annual survival (derived from the monthly survival) for our study population was $0.85^{12} = 0.15$ for the 1st study, and $0.81^{12} = 0.07$ for the 2nd study; these survival rates are substantially lower than those reported for other species of flying squirrels (Gomez et al. 2005; Lampila et al. 2009; Lehmkuhl et al. 2006). However, it should be noted that these apparent survival estimates confound mortality and permanent emigration, and none of these studies addressed whether and to what extent the

estimates of apparent survival were influenced by emigration. Indeed, the relatively low survival rate for the southern flying squirrels in our study site is somewhat surprising, given the widely held belief that southern flying squirrel populations are increasing in numbers in most of its range and are considered a threat for conservation of cavity-nesting endangered species such as red cockaded woodpeckers (Borgo et al. 2010; Werner and Peacor 2003). The causes of the rather substantial differences in survival among flying squirrel species (particularly between northern and southern flying squirrels) remain unclear.

Among the 3 factors considered in this study (fire, food, and mammalian predator exclusion), only fire was found to substantially influence survival of southern flying squirrels. Monthly apparent survival was higher for up to 9 months after the burn in all 4 sites during all 3 burn years. The positive impact of fire on arboreal flying squirrel survival might be due to a decreased structural complexity of understory vegetation after fire events, which facilitates locomotion and increases the ability of flying squirrels to detect and avoid predators (Bendel and Gates 1987; Metcalfe 1984; Schooley et al. 1996). Our analyses revealed that the positive effect of fire on squirrel survival may last up to 9 months. We note, however, that we were not able to model the effect of fire lasting >9 months due to a potentially confounding effect of year. Thus, we cannot conclude that the survival effect of prescribed fire does not extend beyond 9 months. Survival of ground-dwelling small mammals on the same study sites either showed no response (cotton mice and oldfield mice—Karmacharya et al. 2012; Morris et al. 2011a) or was negatively affected by prescribed fire (cotton rats—Karmacharya et al. 2012; Morris et al. 2011b). These differences may have occurred because of differences in resource needs between the southern flying squirrel, an arboreal species, and the ground-dwelling small mammals.

We also observed substantial temporal variation in monthly apparent survival, with the highest survival in 2009 and lowest in 2007. Interestingly, both 2007 and 2009 were burn years. We do not know the reason for a particularly low survival in 2007, but these results likely reflect the fact that annual variation in survival, due perhaps to stochastic variation in environmental factors, can potentially overshadow the positive effect of prescribed fire on the survival of the southern flying squirrel. We believe that rainfall in particular may influence flying squirrel survival. The year of lowest survival also was the year of least rainfall and the year with greatest survival received the most rain. In fact, when rainfall and survival are ranked by year, they correspond nearly perfectly across all years of this study. Unfortunately we lack the data (i.e., data on vegetation or mast) to determine a specific mechanism by which rainfall may have influenced survival.

There was no strong evidence that food supplementation substantially affected survival. From the use of remote cameras, we know that southern flying squirrels do consume the supplemental food in our study site (see “Materials and Methods” [Morris et al. 2011b]). Food supplementation studies

at the same site revealed that supplemental food positively affected survival of other small mammals (cotton rats, cotton mice, and oldfield mice) and rates of transition to reproductive states (Morris et al. 2011a, 2011b). Previous studies have shown that supplemental feeding had either no effect or only marginal effects on population parameters of squirrel species (Havera and Nixon 1980; Klenner and Krebs 1991; Sullivan 1990). The lack of response to supplemental food by the flying squirrels suggests that food was not limiting southern flying squirrels during our study, although we could not objectively test for potential effects of supplemental food on reproductive parameters. An alternative explanation is that supplemental food in our study was provided from July to October, a period when the availability of natural food resources is generally high. Long-term food supplementation studies over multiple seasons would be needed to conclusively test the effect of food supplementation on southern flying squirrel population parameters.

Models with and without the effect of mammalian predator exclusion received similar support, and monthly apparent survival did not differ substantially between mammalian predator exclusion and control sites. These results suggest no major impact of mammalian mesopredators on the survival of southern flying squirrels in our study site. Although mammalian mesopredators were excluded from the predator exclusion sites, access to these sites by avian predators and snakes was not affected; indeed, raptors and snakes, rather than mammalian mesocarnivores, are perhaps more important predators of these cavity-dwelling arboreal mammals (Carey et al. 1992; Laves and Loeb 1999; Mitchell et al. 1999; Rudolph et al. 1990) and this lack of response to mammalian predator exclusion was not surprising. Scat analysis of bobcats (*Lynx rufus*) at the present study site reported that <10% of the bobcat scats contained southern flying squirrel remains (Godbois et al. 2003); other studies have reported flying squirrels as the most common prey species for the spotted owl (*Strix occidentalis*—Carey et al. 1992; Forsman et al. 1984). Studies have shown high use of cavity nests (Holloway and Malcolm 2007) and nest depredation of various avian species by southern flying squirrels (Goertz et al. 1975; Kilham 1968; Stabb et al. 1989). To avoid larger predators, southern flying squirrels prefer cavities that are not yet enlarged by other cavity users (Loeb 1993; Muul 1968; Rudolph et al. 1990), and this makes them especially vulnerable to snake predation because the small entrance hole prevents their escape once the cavity is intruded by snakes.

It is intriguing that the southern flying squirrel had a lower apparent survival rate than the northern flying squirrel (a threatened species in parts of its range), considering the fact that the former is often considered a pest species. It is well known that species characterized by early maturity and high reproductive rates have potential for rapid population growth in favorable circumstances (Oli and Dobson 1999, 2003, 2005; Pianka 1970). The ability of southern flying squirrel populations to increase rapidly may, therefore, be facilitated by high reproductive rates or early maturity, or both, rather than high

survival rates. In fact, flying squirrels can produce more than 1 litter per year, litter size can range from 2 to 7 pups (Dolan and Carter 1977; Gilmore and Gates 1985; Muul 1969; Stapp and Mautz 1991), and they reproduce throughout the year in our study site. A detailed study of their population ecology is needed to understand the demographic basis and environmental effects of southern flying squirrel population dynamics.

ACKNOWLEDGMENTS

We thank J. Rutledge for assistance with fieldwork and logistic arrangements and many technicians who contributed to the collection of data. Our warmest thanks are extended to M. Simmons, who worked diligently to manage our database. Prescribed burns were executed by J. Atkinson, S. Smith, C. Eddins, and B. Williamson. Fieldwork was funded by the Jones Ecological Research Center, and the graduate program for BK was supported by the Department of Wildlife Ecology and Conservation, University of Florida, and the United States Foreign Fulbright Program Division.

LITERATURE CITED

- ATKINSON, J. B., B. JEAN, AND S. ROBERT. 1996. Operational longleaf pine management at Ichauway. Pp. 43–45 in Longleaf pine: a regional perspective of challenges and opportunities (J. S. Kush, ed.). Longleaf Alliance, Andalusia, Alabama.
- BENDEL, P. R., AND J. E. GATES. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). *Journal of Mammalogy* 68:243–255.
- BORGO, J. S., M. R. CONOVER, AND L. M. CONNER. 2010. Flying squirrel removal does not reduce their use of simulated red-cockaded woodpecker nest clusters. *Southeastern Naturalist* 9:813–820.
- BRADY, M. J., T. S. RISCH, AND F. S. DOBSON. 2000. Availability of nest sites does not limit population size of southern flying squirrels. *Canadian Journal of Zoology* 78:1144–1149.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CAMPBELL, M. T., AND N. A. SLADE. 1995. The effect of maternal mass on litter size and offspring survival in the hispid cotton rat (*Sigmodon hispidus*). *Canadian Journal of Zoology* 73:133–140.
- CAREY, A. B., S. P. HORTON, AND B. L. BISWELL. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 62:223–250.
- COLE, F. R., AND G. O. BATZLI. 1978. Influence of supplemental feeding on a vole population. *Journal of Mammalogy* 59:809–819.
- CONNER, L. M., J. C. RUTLEDGE, AND L. L. SMITH. 2010. Effects of mesopredators on nest survival of shrub-nesting songbirds. *Journal of Wildlife Management* 74:73–80.
- DOLAN, P. G., AND D. C. CARTER. 1977. *Glaucomys volans*. *Mammalian Species* 78:1–6.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* 87:3–64.
- GENTRY, J. B., F. B. GOLLEY, AND M. H. SMITH. 1968. An evaluation of the proposed International Biological Program census method for estimating small mammal populations. *Acta Theriologica* 13:313–327.
- GILMORE, R. M., AND J. E. GATES. 1985. Habitat use by the southern flying squirrel at a hemlock–northern hardwood ecotone. *Journal of Wildlife Management* 49:703–710.
- GLITZENSTEIN, J. S., W. J. PLATT, AND D. R. STRENG. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. *Ecological Monographs* 65:441–476.
- GODBOIS, I. A., L. M. CONNER, AND R. J. WARREN. 2003. Bobcat diet on an area managed for northern bobwhite. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 57:222–227.
- GOERTZ, J. W., R. M. DAWSON, AND E. E. MOWBRAY. 1975. Response to nest boxes and reproduction by *Glaucomys volans* in northern Louisiana. *Journal of Mammalogy* 56:933–939.
- GOMEZ, D. M., R. G. ANTHONY, AND J. P. HAYES. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. *Journal of Wildlife Management* 69:1670–1682.
- HANSEN, L. P., AND G. O. BATZLI. 1979. Influence of supplemental food on local populations of *Peromyscus leucopus*. *Journal of Mammalogy* 60:335–342.
- HAVERA, S. P., AND C. M. NIXON. 1980. Winter feeding of fox and gray squirrel populations. *Journal of Wildlife Management* 44:41–55.
- HOLLOWAY, G. L., AND J. R. MALCOLM. 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. *Journal of Mammalogy* 88:226–233.
- HUBBS, A. H., AND R. BOONSTRA. 1997. Population limitation in arctic ground squirrels: effects of food and predation. *Journal of Animal Ecology* 66:527–541.
- KARMACHARYA, B., J. A. HOSTETLER, L. M. CONNER, G. MORRIS, AND M. K. OLI. 2012. Longleaf pine management practices and their impact on small mammal populations. *Forest Ecology and Management* 271:140–146.
- KILHAM, L. 1968. Reproductive behavior of hairy woodpeckers II. Nesting and habitat. *Wilson Bulletin* 80:286–305.
- KLENNER, W., AND C. J. KREBS. 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. *Journal of Animal Ecology* 60:961–978.
- KREBS, C. J., ET AL. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- LAAKE, J., AND E. REXSTAD. 2009. RMark—an alternative approach to building linear models in MARK. Pp. C1–C115 in Program MARK: a gentle introduction (E. Cooch and G. White, eds.). <http://www.phidot.org/software/mark/docs/book/>. Accessed 15 January 2011.
- LAMPILA, S., R. WISTBACKA, A. MAKELA, AND M. ORELL. 2009. Survival and population growth rate of the threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape. *Ecoscience* 16:66–74.
- LAVES, K. S., AND S. C. LOEB. 1999. Effects of southern flying squirrels *Glaucomys volans* on red-cockaded woodpecker *Picoides borealis* reproductive success. *Animal Conservation* 2:295–303.
- LAYNE, J. N., AND M. A. V. RAYMOND. 1994. Communal nesting of southern flying squirrels in Florida. *Journal of Mammalogy* 75:110–120.
- LEHMKUHL, J. F., K. D. KISTLER, J. S. BEGLEY, AND J. BOULANGER. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. *Ecological Applications* 16:584–600.
- LOEB, S. C. 1993. Use and selection of red-cockaded woodpecker cavities by southern flying squirrels. *Journal of Wildlife Management* 57:329–335.
- MCMANARA, J. M., AND A. I. HOUSTON. 1987. Starvation and predation as factors limiting population size. *Ecology* 68:1515–1519.
- MESERVE, P. L., J. R. GUTIERREZ, AND F. M. JAKSIC. 1993. Effects of vertebrate predation on a caviomorph rodent, the degu (*Octodon*

- degus*), in a semiarid thorn scrub community in Chile. *Oecologia* 94:153–158.
- METCALFE, N. B. 1984. The effects of habitat on the vigilance of shorebirds—is visibility important? *Animal Behaviour* 32:981–985.
- MITCHELL, L. R., L. D. CARLILE, AND C. R. CHANDLER. 1999. Effects of southern flying squirrels on nest success of red-cockaded woodpeckers. *Journal of Wildlife Management* 63:538–545.
- MITCHELL, M. S., R. A. LANCIA, AND E. J. JONES. 1996. Use of insecticide to control destructive activity of ants during trapping of small mammals. *Journal of Mammalogy* 77:1107–1113.
- MORRIS, G., J. HOSTETLER, L. M. CONNER, AND M. OLI. 2011a. Effects of predation, fire, and supplemental feeding on populations of two species of *Peromyscus* mice. *Journal of Mammalogy* 92:934–944.
- MORRIS, G., J. HOSTETLER, L. M. CONNER, AND M. OLI. 2011b. Effects of prescribed fire, supplemental feeding, and mammalian predator exclusion on hispid cotton rat populations. *Oecologia* 165:1005–1016.
- MUUL, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. Miscellaneous Publications of the Museum of Zoology, University of Michigan 134:1–66.
- MUUL, I. 1969. Photoperiod and reproduction in flying squirrels, *Glaucomys volans*. *Journal of Mammalogy* 50:542–549.
- OLI, M. K., AND F. S. DOBSON. 1999. Population cycles in small mammals: the role of age at sexual maturity. *Oikos* 86:557–565.
- OLI, M. K., AND F. S. DOBSON. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161:422–440.
- OLI, M. K., AND F. S. DOBSON. 2005. Generation time, elasticity patterns, and mammalian life histories: a reply to Gaillard et al. *American Naturalist* 166:124–128.
- PIANKA, E. R. 1970. On r- and K-selection. *American Naturalist* 104:592–597.
- PYNE, S. J., P. L. ANDREWS, AND R. D. LAVEN. 1996. Introduction to wildland fire. John Wiley & Sons, Inc., New York.
- RANSOME, D. B., AND T. P. SULLIVAN. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. *Journal of Mammalogy* 78:538–549.
- RANSOME, D. B., AND T. P. SULLIVAN. 2004. Effects of food and dense site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *Journal of Mammalogy* 85:206–215.
- R DEVELOPMENT CORE TEAM. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>. Accessed 15 January 2011.
- RISCH, T. S., AND M. J. BRADY. 1996. Trap height and capture success of arboreal small mammals: evidence from southern flying squirrels (*Glaucomys volans*). *American Midland Naturalist* 136:346–351.
- RUDOLPH, D. C., H. KYLE, AND R. N. CONNER. 1990. Red-cockaded woodpeckers vs. rat snakes—the effectiveness of resin barrier. *Wilson Bulletin* 102:14–22.
- SAWYER, S. L., AND R. K. ROSE. 1985. Homing in and ecology of the southern flying squirrel *Glaucomys volans* in southern Virginia. *American Midland Naturalist* 113:238–244.
- SCHNELL, J. H. 1968. Limiting effects of natural predation on experimental cotton rat populations. *Journal of Wildlife Management* 32:698–711.
- SCHOOLEY, R. L., P. B. SHARPE, AND B. VANHORNE. 1996. Can shrub cover increase predation risk for a desert rodent? *Canadian Journal of Zoology* 74:157–163.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SINCLAIR, A. R. E., AND R. P. PECH. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos* 75:164–173.
- SMITH, J. K. 2000. Wildland fire in ecosystems. Effects of fire on fauna. Rocky Mountain Research Station, United States Department of Agriculture Forest Service, General Technical Report, pp. i–v fl 1–83.
- STABB, M. A., M. E. GARTSHORE, AND P. L. AIRD. 1989. Interactions of southern flying squirrels, *Glaucomys volans*, and cavity-nesting birds. *Canadian Field-Naturalist* 103:401–403.
- STAPP, P., AND W. M. MAUTZ. 1991. Breeding habits and postnatal-growth of the southern flying squirrel (*Glaucomys volans*) in New Hampshire. *American Midland Naturalist* 126:203–208.
- SULLIVAN, T. P. 1990. Responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. *Journal of Mammalogy* 71:579–590.
- TAITT, M. J., AND C. J. KREBS. 1983. Predation, cover, and food manipulations during a spring decline of *Microtus townsendii*. *Journal of Animal Ecology* 52:837–848.
- VAN LEAR, D. H., W. D. CARROLL, P. R. KAPELUCK, AND R. JOHNSON. 2005. History and restoration of the longleaf pine–grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211:150–165.
- WEIGL, P. D., M. A. STEELE, L. J. SHERMAN, AND J. C. HA. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. *Bulletin of the Tall Timbers Research Station* 24:1–93.
- WERNER, E. E., AND S. D. PEACOR. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, supplement:120–138.

Submitted 21 March 2012. Accepted 24 September 2012.

Associate Editor was Paul T. Stapp.

APPENDIX I

Model-averaged estimates of monthly apparent survival rates, *SE* and 95% confidence intervals of southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia, from 2005 to 2009. The model set used to derive averaged estimates is shown in Table 1a. Table includes ϕ (monthly survival rate), standard error of the survival estimate (*SE*), 95% lower confidence limit (*LCL*), and 95% upper confidence limit (*UCL*).

Year	Sex	Site	ϕ	<i>SE</i>	<i>LCL</i>	<i>UCL</i>
2005	Female	1	0.887	0.059	0.714	0.961
2006	Female	1	0.800	0.070	0.630	0.904
2007	Female	1	0.561	0.127	0.317	0.779
2008	Female	1	0.752	0.073	0.584	0.868
2009	Female	1	0.920	0.055	0.728	0.980
2005	Male	1	0.895	0.063	0.698	0.969
2006	Male	1	0.815	0.079	0.612	0.924
2007	Male	1	0.588	0.146	0.305	0.823
2008	Male	1	0.769	0.088	0.557	0.898
2009	Male	1	0.927	0.054	0.724	0.984
2005	Female	2	0.934	0.031	0.841	0.974
2006	Female	2	0.874	0.046	0.753	0.940
2007	Female	2	0.690	0.084	0.507	0.828
2008	Female	2	0.841	0.045	0.732	0.911
2009	Female	2	0.951	0.037	0.804	0.989
2005	Male	2	0.941	0.028	0.855	0.977
2006	Male	2	0.888	0.037	0.794	0.943
2007	Male	2	0.717	0.073	0.556	0.837
2008	Male	2	0.858	0.038	0.767	0.917
2009	Male	2	0.957	0.031	0.836	0.990
2005	Female	3	0.927	0.038	0.809	0.974
2006	Female	3	0.862	0.053	0.724	0.937
2007	Female	3	0.666	0.102	0.449	0.830
2008	Female	3	0.826	0.047	0.715	0.900
2009	Female	3	0.946	0.041	0.785	0.988
2005	Male	3	0.934	0.037	0.814	0.979
2006	Male	3	0.877	0.048	0.748	0.945
2007	Male	3	0.693	0.099	0.475	0.849
2008	Male	3	0.843	0.046	0.732	0.914
2009	Male	3	0.953	0.036	0.808	0.990
2005	Female	4	0.909	0.046	0.769	0.967
2006	Female	4	0.833	0.062	0.676	0.922
2007	Female	4	0.612	0.104	0.400	0.788
2008	Female	4	0.790	0.059	0.652	0.884
2009	Female	4	0.934	0.046	0.767	0.984
2005	Male	4	0.916	0.048	0.762	0.974
2006	Male	4	0.847	0.065	0.675	0.937
2007	Male	4	0.639	0.115	0.400	0.824
2008	Male	4	0.808	0.068	0.641	0.908
2009	Male	4	0.941	0.043	0.775	0.987

APPENDIX II

Model-averaged estimates of monthly apparent survival rates, *SE* and 95% confidence intervals of southern flying squirrels with and without the effect of prescribed fire in the Jones Ecological Research Center, Newton, Georgia, from 2005 to 2009. The model set used to derive averaged estimates is shown in Table 2a. See Appendix I for column definitions. There was no capture occasion 9 months after the fire event in the year 2009.

Period	Year	Site	ϕ	<i>SE</i>	<i>LCL</i>	<i>UCL</i>
0–3 months postfire	2005	1	0.954	0.062	0.567	0.997
3–6 months postfire	2005	1	0.951	0.063	0.573	0.996
6–9 months postfire	2005	1	0.886	0.088	0.583	0.977
Nonfire	2005	1	0.800	0.102	0.533	0.933
0–3 months postfire	2007	1	0.650	0.180	0.282	0.897
3–6 months postfire	2007	1	0.642	0.180	0.278	0.893
6–9 months postfire	2007	1	0.418	0.240	0.094	0.832
Nonfire	2007	1	0.241	0.195	0.038	0.719
0–3 months postfire	2009	1	0.951	0.059	0.616	0.996
3–6 months postfire	2009	1	0.953	0.059	0.609	0.996
Nonfire	2009	1	0.913	0.080	0.591	0.987
0–3 months postfire	2005	2	0.981	0.026	0.767	0.999
3–6 months postfire	2005	2	0.980	0.027	0.772	0.999
6–9 months postfire	2005	2	0.953	0.037	0.799	0.991
Nonfire	2005	2	0.912	0.051	0.747	0.973
0–3 months postfire	2007	2	0.828	0.105	0.532	0.953
3–6 months postfire	2007	2	0.822	0.107	0.525	0.951
6–9 months postfire	2007	2	0.622	0.234	0.190	0.920
Nonfire	2007	2	0.441	0.258	0.092	0.860
0–3 months postfire	2009	2	0.980	0.026	0.786	0.999
3–6 months postfire	2009	2	0.981	0.025	0.782	0.999
Nonfire	2009	2	0.966	0.035	0.785	0.995
0–3 months postfire	2005	3	0.977	0.033	0.699	0.999
3–6 months postfire	2005	3	0.976	0.034	0.703	0.999
6–9 months postfire	2005	3	0.942	0.052	0.719	0.990
Nonfire	2005	3	0.893	0.072	0.655	0.973
0–3 months postfire	2007	3	0.794	0.134	0.437	0.950
3–6 months postfire	2007	3	0.788	0.136	0.431	0.948
6–9 months postfire	2007	3	0.575	0.253	0.150	0.912
Nonfire	2007	3	0.390	0.261	0.069	0.846
0–3 months postfire	2009	3	0.976	0.033	0.715	0.998
3–6 months postfire	2009	3	0.977	0.033	0.710	0.999
Nonfire	2009	3	0.957	0.046	0.710	0.995
0–3 months postfire	2005	4	0.965	0.046	0.645	0.998
3–6 months postfire	2005	4	0.963	0.048	0.646	0.997
6–9 months postfire	2005	4	0.911	0.074	0.634	0.984
Nonfire	2005	4	0.841	0.092	0.577	0.954
0–3 months postfire	2007	4	0.711	0.148	0.375	0.910
3–6 months postfire	2007	4	0.704	0.149	0.368	0.906
6–9 months postfire	2007	4	0.478	0.253	0.111	0.870
Nonfire	2007	4	0.294	0.230	0.045	0.785
0–3 months postfire	2009	4	0.963	0.046	0.673	0.997
3–6 months postfire	2009	4	0.965	0.045	0.667	0.997
Nonfire	2009	4	0.933	0.063	0.657	0.990

APPENDIX III

Model-averaged estimates of monthly apparent survival rates, *SE* and 95% confidence intervals of southern flying squirrels at control and mammalian predator exclosures in the Jones Ecological Research Center, Newton, Georgia, from 2005 to 2010. The model set used to derive averaged estimates is shown in Tables 2b and 4b. See Appendix I for column definitions.

Year	Site	Predation	ϕ	<i>SE</i>	<i>LCL</i>	<i>UCL</i>
2005	1	No	0.850	0.068	0.667	0.941
2005	1	Yes	0.866	0.058	0.710	0.945
2006	1	No	0.753	0.077	0.574	0.873
2006	1	Yes	0.777	0.068	0.618	0.882
2007	1	No	0.472	0.124	0.252	0.704
2007	1	Yes	0.505	0.115	0.292	0.716
2008	1	No	0.698	0.075	0.536	0.823
2008	1	Yes	0.725	0.069	0.572	0.839
2009	1	No	0.908	0.065	0.681	0.979
2009	1	Yes	0.918	0.059	0.705	0.981
2010	1	No	0.618	0.081	0.453	0.760
2010	1	Yes	0.556	11.018	0.000	1.000
2005	2	No	0.939	0.026	0.862	0.974
2005	2	Yes	0.946	0.025	0.872	0.978
2006	2	No	0.892	0.034	0.804	0.943
2006	2	Yes	0.904	0.034	0.813	0.953
2007	2	No	0.707	0.074	0.545	0.830
2007	2	Yes	0.733	0.072	0.571	0.850
2008	2	No	0.862	0.034	0.783	0.916
2008	2	Yes	0.876	0.037	0.783	0.933
2009	2	No	0.964	0.028	0.844	0.993
2009	2	Yes	0.968	0.026	0.851	0.994
2010	2	No	0.849	0.031	0.777	0.900
2010	2	Yes	0.809	0.043	0.710	0.880
2005	3	No	0.923	0.044	0.781	0.976
2005	3	Yes	0.932	0.038	0.809	0.978
2006	3	No	0.867	0.059	0.705	0.946
2006	3	Yes	0.881	0.052	0.735	0.952
2007	3	No	0.655	0.121	0.399	0.845
2007	3	Yes	0.685	0.110	0.444	0.855
2008	3	No	0.831	0.053	0.702	0.912
2008	3	Yes	0.849	0.049	0.726	0.922
2009	3	No	0.955	0.039	0.779	0.992
2009	3	Yes	0.960	0.036	0.796	0.993
2010	3	No	0.788	0.102	0.529	0.925
2010	3	Yes	0.750	0.093	0.533	0.887
2005	4	No	0.890	0.057	0.723	0.961
2005	4	Yes	0.902	0.049	0.758	0.965
2006	4	No	0.813	0.077	0.616	0.922
2006	4	Yes	0.832	0.069	0.653	0.929
2007	4	No	0.560	0.119	0.332	0.766
2007	4	Yes	0.592	0.108	0.377	0.777
2008	4	No	0.767	0.073	0.595	0.881
2008	4	Yes	0.790	0.068	0.626	0.894
2009	4	No	0.934	0.051	0.738	0.986
2009	4	Yes	0.941	0.046	0.757	0.988
2010	4	No	0.800	0.055	0.670	0.887
2010	4	Yes	0.752	8.016	0.000	1.000

APPENDIX IV

Model-averaged estimates of monthly apparent survival rates, *SE* and 95% confidence intervals of southern flying squirrels in the Jones Ecological Research Center, Newton, Georgia, during the year 2010. The model set used to derive averaged estimates is shown in Table 3a. See Appendix I for column definitions.

Year	Sex	Site	ϕ	<i>SE</i>	<i>LCL</i>	<i>UCL</i>
2010	Female	1	0.681	0.116	0.429	0.859
2010	Male	1	0.689	0.112	0.443	0.861
2010	Female	2	0.821	0.030	0.754	0.873
2010	Male	2	0.827	0.032	0.754	0.881
2010	Female	3	0.770	0.076	0.590	0.886
2010	Male	3	0.775	0.081	0.582	0.895
2010	Female	4	0.799	0.048	0.689	0.877
2010	Male	4	0.805	0.050	0.690	0.885

APPENDIX V

Model-averaged estimates of monthly apparent survival rates, *SE* and 95% confidence intervals of southern flying squirrels with and without food supplementation in the Jones Ecological Research Center, Newton, Georgia, during the year 2010. The model set used to derive averaged estimates is shown in Table 4a. See Appendix I for column definitions.

Year	Food supplementation	Site	ϕ	<i>SE</i>	<i>LCL</i>	<i>UCL</i>
2010	No	1	0.654	0.106	0.429	0.826
2010	Yes	1	0.603	0.088	0.425	0.757
2010	No	3	0.760	0.088	0.551	0.892
2010	Yes	3	0.715	0.122	0.436	0.891