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Food resources and predation can influence various aspects of the ecology of small mammals, including movement and space-use patterns. We used radiotelemetry to examine experimentally how supplemental feeding and mammalian predator exclusion affected size and exclusivity of hispid cotton rat (*Sigmodon hispidus*) home ranges. Supplemental feeding had no effect on home-range size, and exclusivity was not influenced by either treatment. However, predator exclusion was associated with increased home-range sizes, indicating a behavioral response to perceived predation risk. We suggest that this behavioral response reflects a trade-off between predation risk and space-use patterns.

Key words: food supplementation, hispid cotton rat, home range, nonconsumptive effects, predation, *Sigmodon hispidus*, space-use pattern

Food resource availability and predation can influence various aspects of the ecology of small mammals. Field experiments have shown that many species of small mammals reduce home-range size in the presence of supplemental food (Boutin 1990), although this might at times be a response to increased population densities rather than to supplemental food itself (Desy et al. 1990). Food addition also has been associated with changes in intraspecific aggression (Desy et al. 1990).

Studies examining the effects of predator exclusion on space use by small mammals have indicated that predation can influence home-range size and habitat use (Arthur et al. 2004; Desy et al. 1990; Dickman 1992). However, these results have been inconsistent. Desy et al. (1990) found that voles had smaller home ranges in areas where predators were allowed access than in areas where predators were excluded, whereas Yunger (2004) found that predator exclusion had a numerical effect on voles but had no effect on home-range size or overlap. Yunger (2004) did observe a decrease in home-range size in white-footed mice (*Peromyscus leucopus*) but believed this to be due to competitive interactions with increased vole population densities.

Although food availability and predation risk individually can have large impacts on the ecology of small mammals, a great deal of support also exists for ecological effects of interactions between these factors (Abrams 1982, 1984;

McNamara and Houston 1987). Such interactions can stem from the likelihood that foraging puts individuals at greater risk of predation. An individual must make trade-offs between the need to acquire food and the need to stay safe from predators. Optimally, an individual should minimize risk of death from predation while maximizing food intake. A large body of research suggests such trade-offs are common (Lima and Dill 1989). Trade-offs also can be made between predation risk and other behaviors, such as seeking out reproductive opportunities (Clark and Mangel 2000; Lima and Dill 1989).

The objective of this study was to examine experimentally how predation and supplemental feeding affected size and exclusivity of home ranges of hispid cotton rats (*Sigmodon hispidus*) in a longleaf pine (*Pinus palustris*) ecosystem. Home-range estimates reflect movement patterns; animals that move less generally have smaller home ranges. Therefore, if predation or feeding treatments affect movement patterns in cotton rats, it is likely that this will be reflected by different estimates of home-range sizes between treatments. Estimates of exclusivity can provide insight into social interactions. Previous studies have measured aggression between rodents by observing staged dyadic encounters between field-captured

animals (Desy et al. 1990). Measures of home-range exclusivity also can be used to assess tolerance of individuals for one another and are less invasive than staged encounters.

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 (*P. palustris*) and wiregrass (*Aristida beyrichiana*) ecosystem. Longleaf pine ecosystems are characterized by a low-density longleaf pine overstory, a diverse, herbaceous groundcover, and an open, parklike midstory (Van Lear et al. 2005). Hardwood tree species occur at low densities. Frequent, low-intensity fire is a key ecological process. Consequently, application of prescribed fire is a primary management tool throughout Ichauway; most sites are burned on a 2-year rotation (J. B. Atkinson, J. W. Jones Ecological Research Center, pers. comm.).

Cotton rats are solitary rodents found abundantly across the southeastern and south-central United States. Cotton rats generally are described as crepuscular, but they also can 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), for protection from a wide range of avian, mammalian, and snake predators. Herbaceous vegetation also is consumed as a primary food source and used in nest construction. Predation is the most common cause of death among cotton rats (Derrick 2007; Wiegert 1972), and predation pressure is so strong that cotton rat populations experience near complete turnover in as little as 5–8 months (Goertz 1964).

Experimental design.—In 2002 the Jones Center constructed 4 mammalian predator exclosures and established 4 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 and snakes to pass through). Predators excluded from these areas include bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), nine-banded armadillos (*Dasypus novemcinctus*), striped skunks (*Mephitis mephitis*), and spotted skunks (*Spilogale putorius*). Although mammalian predators occasionally enter exclosures, regular monitoring by track counts and thermal camera surveys indicates significantly fewer mammalian predators in exclosures than in controls (from June 2007 to August 2009, 74 mammalian mesopredator detections in controls and 7 detections in exclosures—Conner et al. 2010). In February 2009 all plots were burned according to Ichauway's burn plan, which has these study areas on a 2-year burn rotation.

From June of 2007 through August of 2009, 2 exclosure and 2 control grids were selected randomly to receive a supplemental feeding treatment consisting of placing 113 g of rabbit chow in cans at alternate stations on small-mammal trapping grids in selected sites (see below). Food was replaced every other week. Empty cans were placed on nonfeeding grids to mitigate any effects related to the presence of the cans themselves (e.g., providing refugia). 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 (Morris et al. 2010). We found no evidence that cans were defended by individuals of any species. This assessment was based on regular observations of cans being visited not only by multiple species but by multiple individuals of the same species (individuals were distinguished by features such as coloration, body size, and presence or absence of ear tags).

Field methods.—Each control and exclosure contained a 12 × 12 small-mammal trapping grid with 15-m spacing between stations. Pairs of grids were trapped 8 times per year (twice per season) from July 2007 through the June 2009 using Sherman live traps (model XLK; H. B. Sherman Traps, Inc., Tallahassee, Florida). A small amount of a granular insecticide (Talstar Nursery Granular Insecticide; FMC Corporation, Philadelphia, Pennsylvania) was sprinkled around each trap to prevent deaths due to fire ants. Newly captured animals were marked individually with metal ear tags (National Band and Tag Company, Newport, Kentucky). Data recorded for all captures included location, species, sex, body mass, age (adult or juvenile, based on body mass; we considered cotton rats ≥50 g to be adults—Bergstrom and Rose 2004), reproductive condition (for males, testes descended or not; for females, pregnant or lactating or both, or not), and hind-foot measurement.

In 4 of the 8 study plots (1 fed predator exclosure, 1 unfed predator exclosure, 1 fed predator control, and 1 unfed predator control plot) cotton rats weighing ≥90 g were anesthetized with isoflurane (Minrad Inc., Bethlehem, Pennsylvania) and fitted with 4.5-g radiocollars (Advanced Telemetry Systems, Isanti, Minnesota; Sirtrack Wildlife Tracking Solutions, Havelock North, New Zealand; and Telenax, Playa del Carmen, Mexico). Following recovery, rats were released at their capture sites. Collared rats were located by triangulation or homing a minimum of 3 times per week and located visually once a week to confirm status as alive or dead. Rats were located using TRXC-2000S (Wildlife Materials, Murpheysboro, Illinois), R-1000 (Communication Specialists, Inc., Orange, California), or R-2000 (Advanced Telemetry Systems) receivers. When triangulating, we used a minimum of 2 bearings, which generally were taken at distances ≤50 m of collared rats. Telemetry accuracy tests indicated that bearings taken from such distances were within 5 m of transmitters. Because a distance of 5 m is minimal compared to the overall home-range size, we did not incorporate bearing errors into location estimates. When homing, we found that rats generally did not flush until

observers were within 1–2 m; therefore, we recorded locations of such animals where they were 1st spotted and do not believe homing influenced space use of these animals. Additionally, when homing, we were able to tell reliably, based on signal strength, when we were within 1–5 m of collared rats and avoided flushing animals unless we needed to do so to confirm status as alive. Collaring and tracking began in July 2007 and continued through August 2009. 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 telemetry data.—Home ranges were estimated using 95% minimum convex polygons (MCPs) and, for purpose of comparison to other studies, 95% fixed kernel methods. To avoid short sampling intervals and small sample sizes, which can contribute to inaccurate home-range estimates (Swihart and Slade 1985a, 1985b), we followed the recommendations of Cameron and Spencer (1985) and Swihart and Slade (1985b) and estimated home ranges only for rats that had a minimum of 25 locations with at least 4.5 h between locations. An examination of correlation between home-range size and the number of locations used to estimate home range showed that home-range size was not significantly correlated ($P > 0.05$) with number of locations when ≥ 25 locations were used (SAS procedure PROC CORR—SAS Institute Inc. 2004). This was true for both MCP and fixed kernel home-range estimates.

The MCP estimates were generated using the program CALHOME (Kie et al. 1994). Kernel estimates were generated in ArcGIS 9 (Environmental Systems Research Institute, Inc. 2005) using the Hawth's tools extension (Beyer 2004). Kernel bandwidth was specified by least-squares cross validation (Seaman and Powell 1996) for all rats, with the exception of 8, which were found repeatedly at the same location(s) (usually a nest or burrow). To prevent bias such behavior can create in home-range estimates using least-squares cross validation to determine bandwidth (Seaman and Powell 1996), the bandwidth for these 8 rats was specified using the mean least-squares cross-validation–generated bandwidth for all other rats combined. Home-range estimates were calculated from composite data and represented the home range for the duration of sampling for a given cotton rat.

A *t*-test examining difference in home-range size between males and females (using 95% MCP estimates) indicated that male rats had significantly larger home ranges than females ($P < 0.001$, $t_{73} = -4.13$); therefore, males and females were considered separately in further analysis. Effects of feeding, predation, and the interaction of these treatments on MCP home-range estimates were examined using a 2-way analysis of variance (ANOVA; SAS procedure PROC GLM—Schabenberger and Pierce 2002). MCP estimates were log transformed to meet normality assumptions. ANOVA assumptions, including equal variance and normality of residuals, were checked by examining plots of residuals versus predictions and normal probability plots. A Kolmogorov–Smirnov test for normality also indicated the log-transformed data met normality assumptions ($P > 0.15$).

Fire effects were not considered in these analyses because all collared rats died or emigrated from the study sites within 2 weeks of the fires. We were unable to maintain collared cotton rats in the burned areas until vegetation had made significant recovery (around April–May, depending on the site).

Home-range exclusivity was estimated by identifying all pairs of rats that lived during the same period and had overlapping MCP home ranges. For this analysis we used 95% MCP estimates generated for all rats with a minimum of 15 locations. Unlike home-range estimation, which is sensitive to number of locations (Swihart and Slade 1985a), this analysis was intended to measure tolerance of neighboring rats for each other and is less likely to be influenced by number of locations. MCPs generated using 15 locations were sufficient to determine if 2 rats lived in close proximity to each other. Because MCPs only get larger with the inclusion of more points, it is impossible for rats that have overlapping home ranges with 15 locations not to have overlapping home ranges with the inclusion of additional points.

Distances between pairs of such individuals located by radiotelemetry within 30 min of each other were measured in ArcGIS 9. Distances between randomly selected locations for each pair also were measured. The differences between averaged distances were calculated (average real − average random distance) for each pair to generate an estimate of exclusivity. Positive differences are interpreted as avoidance by each individual of the other individual in a pair, whereas negative differences indicated an affinity. Effects of treatments on this measure were examined using a 2-way ANOVA implemented in PROC GLM in SAS. ANOVA assumptions, including equal variance and normality of residuals, were checked by examining plots of residuals versus predictions and normal probability plots. A Kolmogorov–Smirnov test for normality also indicated the data met normality assumptions ($P > 0.15$). Independent variables included in these models were type of pairing (male–male, female–female, and male–female), feeding treatment, predation treatment, and interactions of type of pairing with feeding and predation treatments (2-way interactions only).

RESULTS

A total of 279 cotton rats was collared during this study. Average home-range size was 3,565 m^2 (range 685–9,814 m^2) for female rats ($n = 37$) using MCP and 6,344 m^2 (range 888–19,627 m^2) using fixed kernel methods. For males ($n = 38$) average home ranges were 8,388 m^2 (range 480–28,240 m^2) and 15,241 m^2 (range 974–47,808 m^2) using MCP and kernel methods, respectively. Clearly, kernel estimates were substantially larger than MCP estimates. Based on our knowledge of the areas actually used by these rats and the areas projected to be included in each rat's home range using MCP and kernel

TABLE 1.—Factors influencing home-range size of cotton rats in southwestern Georgia using 95% minimum convex polygon (MCP) estimates. Two-way ANOVA results are presented. Home-range estimates were log-transformed for this analysis. Food treatment levels were supplemental feeding and control (no supplemental feeding). Predator treatment levels were mammalian predator exclusion and control (no predator exclusion). MS = mean square.

Sex	Source	d.f.	MS	F	P
Males	Food	1, 34	0.13	0.75	0.391
	Predation	1, 34	1.25	7.51	0.010
	Food*predation	1, 34	0.01	0.04	0.838
Females	Food	1, 33	>0.01	0.04	0.833
	Predation	1, 33	0.21	3.40	0.074
	Food*predation	1, 33	0.02	0.35	0.558

estimates, we believe MCP estimates provide a more accurate picture of actual space use for these rats. For the purposes of this study home-range size estimates are of less importance than comparison of home-range sizes between treatments. Therefore, analyses and discussion focus on results based on MCP estimates.

Home-range analysis.—A total of 75 collared rats had sufficient locations for home-range analysis. The average number of locations per home range ($\pm$ *SE*) was 40.1 $\pm$ 1.8 (range 25–92). The only significant treatment effect on home-range size was an effect of the predator treatment (Table 1). Examination of least-square means (LSMs) revealed that males in predator exclosures had larger home ranges (LSM = 8,934 m², 95% confidence interval [95% *CI*] = 5,582–14,298 m²) than males in controls (LSM = 3,827, 95% *CI* = 2,522–5,807 m²). Female rats also had larger home ranges in the exclosures (LSM = 3,739, 95% *CI* = 2,764–5,059 m²) compared to the controls (LSM = 2,595, 95% *CI* = 1,986–3,390 m²), but this difference was only marginally nonsignificant. Neither feeding nor the interaction of feeding and predator treatments significantly affected home-range size of either sex (Table 1). The LSM male home ranges were 6,688 m² (95% *CI* = 4,408–10,148 m²) in feeding areas compared to 5,112 m² (95% *CI* = 3,194–8,182 m²) in nonfeeding areas. The LSM female home ranges were 3,050 m² (95% *CI* = 2,255–4,126 m²) in feeding areas compared to 3,181 m² (95% *CI* = 2,435–4158 m²) in nonfeeding areas.

Home-range exclusivity analysis.—A total of 356 pairs of rats had overlapping home ranges during the same time period. Analysis of home-range exclusivity indicated no effect of type of pairing (male–male, female–female, or male–female), treatment, or interactions of type of pairing and treatment on spacing between rats (Table 2). The mean difference ($\pm$ *SE*) between real and random distances for female–female pairs was −3.50 $\pm$ 1.68 m. For male–male and male–female pairs the difference was −0.16 $\pm$ 2.14 m and −0.05 $\pm$ 1.25 m, respectively. For rats in predator exclosures and controls the difference was −0.26 $\pm$ 1.41 m and −1.04 $\pm$ 1.37 m, respectively. For rats in feeding and nonfeeding plots, the

TABLE 2.—Factors influencing home-range exclusivities of cotton rats in sites treated with supplemental feeding and mammalian predator exclusion in southwestern Georgia from June 2007 to August 2009. Two-way ANOVA results are presented. Pair type refers to whether pairs were female–female, male–male, or male–female. Food treatment levels were supplemental feeding and control (no supplemental feeding). Predator treatment levels were mammalian predator exclusion and control (no predator exclusion). MS = mean square.

Source	d.f.	MS	F	P
Pair type	2, 169	82.190	0.48	0.620
Food	1, 169	9.289	0.05	0.816
Predation	1, 169	17.267	0.10	0.751
Type*food	2, 169	347.416	2.03	0.135
Type*predation	2, 169	120.604	0.70	0.496

difference was −0.90 $\pm$ 1.52 m and −0.46 $\pm$ 1.27, respectively.

DISCUSSION

Predator exclusion was associated with increased home-range sizes. This effect was more pronounced for males than for females. These results suggest a sublethal predation effect. The best-studied examples of sublethal effects of predation deal with the interplay of food acquisition and predation risk. Foraging increases exposure to predators causing individuals to make trade-offs between the needs to eat and minimize predation risk (Abrams 1982, 1984; McNamara and Houston 1987). Individuals might pass up otherwise acceptable food sources if the food is in an area that carries a high risk of predation unless the individual is food stressed (predation-sensitive foraging—Sinclair and Arcese 1995). The lack of feeding effect on home-range size in our study suggests that cotton rats do not make such a trade-off with respect to mammalian predation (or that we were unable to detect such a trade-off). Instead, we found that male cotton rats, and, to a lesser extent female cotton rats, exhibited a behavioral response to predator exclusion alone. How can this be explained outside of a food context? We suggest that cotton rat reproductive strategies drive this response.

The reproductive output of male cotton rats is likely to be influenced more strongly by access to females than by survival, as is generally the case among species characterized by rapid turnover and maturation for which reproductive output typically makes a proportionally greater contribution to population growth rate than does survival (Oli and Dobson 2003). Male cotton rats are promiscuous, range widely, and have no involvement in raising young and therefore should risk predation to maximize reproductive opportunities. Although female rats are less likely to influence their chances of reproducing by changing space use (because a female rat is likely to be bred regardless of whether she encounters a single male or several), male rats ought to increase fitness by mating with as many females as possible. Maintenance of larger home

ranges should increase the chances of encountering females and thus reproductive opportunities. However, when predation pressure is perceived to be great, male rats appear to restrict movements to reduce predation risk.

Female rats showed a similar, although less pronounced, effect of mammalian predator exclusion on home-range size; however, the driving force behind this behavioral response is likely to differ from that of males. Cotton rats mature and reproduce with extraordinary speed, reaching reproductive maturity within 1–2 months, and take just under a month to gestate. Young become independent within 2 weeks of birth, and a female rat can become pregnant again within 24 h of giving birth (Whitaker and Hamilton 1998). Under ideal circumstances a female rat can complete rearing her 1st litter by 3 months of age and a 2nd shortly after 4 months. However, given the extraordinary predation pressure on cotton rats, to a degree that populations see nearly complete turnover in as little as 5–8 months and 50% turnover in 2 months (Goertz 1964; G. Morris, pers. obs.), a relatively small proportion of female cotton rats is likely to live long enough to raise more than a single litter (but see Bergstrom and Rose 2004). Therefore, survival is likely to be an important component of the overall reproductive output for female cotton rats. Although male rats can increase reproductive fitness by ranging widely to encounter females, females can maximize fitness by surviving long enough to bear multiple litters. Female cotton rats therefore might respond to perceived predation risk by reducing movements that increase exposure to predators.

This does not explain why female rats maintain larger home ranges in areas where predation pressure is perceived to be low (such as in our exclosures) when they are capable of surviving on smaller areas (as observed in our controls). It is possible that female rats engage in a degree of mate selection themselves, or that they benefit from improving their knowledge of the surrounding areas and associated features such as burrows, food sources, or protected areas. Female cotton rats in particular might benefit from knowledge of areas where forbs are present, because forbs often occur at low densities in preferred cotton rat habitat but provide high levels of protein (Randolph et al. 1995). Protein is associated with increased growth and maturation rates and reproductive success in female cotton rats (Cameron and Eshelman 1996). When predation risk is perceived to be low, it could be beneficial for female cotton rats to risk predation to acquire resources such as forbs, which are especially likely to improve fitness. Of course, this scenario begs the question as to why the addition of high-protein supplemental food did not influence space use by cotton rats. It is possible that the rats were not cognizant of the protein content of the supplemental food and maintained behaviors they have adapted to ensure adequate protein intake; specifically, whether forbs make up <1% or 40% of the vegetation in an area, cotton rats consistently consume forbs such that they make up at least 4–5% of the diet, probably to ensure optimal nutrient intake (Kincaid and Cameron 1985). However, Deutsch et al. (1989)

suggested that laboratory rats (*Rattus norvegicus*) have an ability to detect protein content in food sources.

The home-range response to mammalian predator exclusion appears to be a response to perceived predation pressure rather than actual risk. A separate analysis of survival of radio-collared cotton rats showed that survival was similar between predator exclosures and controls (Morris 2010). Mammalian predators caused 27% of known predations in controls and only 5% in exclosures. Avian predators (owls and hawks) caused 31% of predations in controls and 70% in exclosures. Known snake predations accounted for 17% in both exclosures and controls; predations caused by unknown predators accounted for 25% and 12% of predations in controls and exclosures, respectively. Increased avian predation appears to make up for losses when mammalian predators are absent. That cotton rats perceive and respond to the presence of mammalian predators but seem less aware of avian predators could reflect use of the same space by such mammalian predators as by rats and deposition of scents that likely are to be detected easily by rats. The same cannot be said of avian predators.

It is possible that differences between the control and exclosure plots other than the predator treatment itself could be responsible for the differences in home-range sizes observed in our study. For example, if the predator treatment was associated with skewed sex ratios, this also might cause changes in space-use patterns. However, male:female sex ratios in the controls and exclosures were similar (0.96 in controls and 0.98 in exclosures, calculated over the period from January 2005 through June 2009). Similarly, if the predator treatment influenced population densities of cotton rats, this also could affect home-range size, as seen in voles (Desy et al. 1990). In a separate analysis no significant difference in abundance between exclosures and controls was observed (Morris 2010).

As a general caveat, which should also be applied to the analyses discussed below, our results, and the conclusions drawn from them, are confined to adult rats, because we were unable to collar rats weighing <90 g; therefore, we were unable to determine whether juveniles or small adults responded differently to the treatments applied here. Additionally, we recorded locations only during the diurnal period, although cotton rats can be active throughout the day and night. Because many predators of the cotton rat are active during night hours, it is possible that cotton rats behave differently at night than during the day. However, previous telemetry studies carried out on our study site suggest that cotton rats use space similarly during day and night hours (L. M. Conner, pers. obs.).

Our analysis failed to detect treatment- or pairing-type effects on cotton rat home-range exclusivity. Previous studies found that female cotton rats have more exclusive home ranges than males (Cameron et al. 1979b; Fleharty and Mares 1973). Other studies suggest that although males and females have similar degrees of exclusivity overall, individuals are more likely to have more extensive home-range overlap with

individuals of the opposite sex than with individuals of the same sex (mutual antagonism within the sexes—Cameron 1995; Cameron and Spencer 1985). The failure to observe similar effects in our study, at least in part, could be due to different methodologies used to quantify home-range exclusivity.

Cameron (1995) and Cameron and Spencer (1985) estimated overlap for co-occurring rats tracked by radiotelemetry around sunrise and sunset by calculating percent overlap of daily MCP home ranges. Cameron et al. (1979b) and Fleharty and Mares (1973) examined distances between centers of activity of individuals as a measure of exclusivity, although these estimates were based on as few as 3–6 trapping locations.

We used a different method to evaluate the tolerance of cotton rats for each other. Locations were taken by radiotelemetry throughout the diurnal period, and exclusivity was evaluated by comparing distances between co-occurring individuals tracked at the same time as random distances between those individuals. Given the social system of cotton rats, we suggest that our method provides a more accurate means of evaluating interactions between rats. In a large-scale laboratory study Liu (1971) observed that cotton rats had a social system characterized by spatial time-sharing (Getty 1981); cotton rats had highly overlapping home ranges but used areas in the home range at different times of the day. Dominant rats foraged around dawn and dusk, and subordinate rats foraged during day or night hours. Subordinate rats defended only areas immediately around their nests, but dominant rats fought or chased all rats encountered in the home range. Dominant rats tended not to have overlapping home ranges with other dominant rats, because encounters between 2 dominants generally ended with the death of 1 rat or the other. Mating pairs shared nests, although they did not forage together, and females moved to new nests that were defended even from their mates shortly before giving birth and while nursing young (Liu 1971). Because cotton rats use extensively overlapping home ranges, measuring home-range overlap in the manner described by Cameron (1995) and Cameron and Spencer (1985) provides limited insight into agonistic interactions when locations are collected when only a subset of the population is likely to have been active. The exclusivity measure used in our study allows an indirect examination of tolerance of cotton rats for each other in a system where individuals use the same space at different times and are solitary and agonistic toward one another.

It should be noted that Liu (1971) relied completely on laboratory observations. Although these observations were made on a relatively large scale and many of the observed aspects of cotton rat social interactions are supported by field observations made in other studies (Cameron et al. 1979a; Cameron and Spencer 1985; G. Morris, pers. obs.), some aspects of Liu's findings are not well documented in the field and could be artifacts of the laboratory setting.

Social interactions also could have contributed to the differences in observed exclusivities between this study and those that used trapping locations to estimate exclusivity (Cameron et al. 1979b; Fleharty and Mares 1973). Space-use patterns estimated from such studies relied on home ranges and dispersion of centers of activity estimated from trapping locations. However, it has been shown that heavier and dominant cotton rats are trapped more readily than smaller, subordinate rats (Joule and Cameron 1974; Summerlin and Wolfe 1973). As noted by Cameron et al. (1979b), such behavior might skew observations of exclusive areas used by cotton rats when observations are based solely on trapping records.

Evidence exists that agonistic interactions between conspecifics decrease in rodents when supplemental food is provided, although no similar decrease in aggression was observed with respect to predator exclusion (Desy et al. 1990). We were unable to detect changes in tolerance of cotton rats toward each other with predation or feeding treatments. Perhaps the amount of experimentally provided food was insufficient or too widely dispersed to allow a decrease in aggression. Alternatively, the ''very aggressive'' (Liu 1971:65) behavior of cotton rats toward each other might be hardwired to such a degree that our experimental treatments were unable to effect a response, even when applied over >8 generations. This, however, assumes that agonistic behavior of cotton rats is a response to dispersion of food resources or to predation risk, as hypothesized by Liu (1971). Examination of our data suggests that food availability does not influence spatial and agonistic behavior in cotton rats, or that food resources were simply not limiting in the unfed grids. Similarly, given that predation rates remained high in exclosures due to the presence of raptors and snake predators, the predation treatment might not have been sufficient to influence this behavior.

LITERATURE CITED

ABRAMS, P. A. 1982. Functional responses of optimal foragers. American Naturalist 120:382–390.

ABRAMS, P. A. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80–96.

ARTHUR, A. D., R. P. PECH, AND C. R. DICKMAN. 2004. Habitat structure mediates the non-lethal effects of predation on enclosed populations of house mice. Journal of Animal Ecology 73:867–877.

BERGSTROM, B. J., AND R. K. ROSE. 2004. Comparative life histories of Georgia and Virginia cotton rats. Journal of Mammalogy 85:1077–1086.

BEYER, H. L. 2004. Hawth's analysis tools for ArcGIS. http://www. spatialecology.com/htools. Accessed 20 November 2008.

BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68:203–220.

CAMERON, G. N. 1995. Temporal use of home range by the hispid cotton rat. Journal of Mammalogy 76:819–827.

CAMERON, G. N., AND B. D. ESHELMAN. 1996. Growth and reproduction of hispid cotton rats (Sigmodon hispidus) in response to naturally occurring levels of dietary protein. Journal of Mammalogy 77:220–231.

CAMERON, G. N., W. B. KINCAID, AND B. A. CARNES. 1979a. Experimental species removal: temporal activity patterns of Sigmodon hispidus and Reithrodontomys fulvescens. Journal of Mammalogy 60:195–197.

CAMERON, G. N., W. B. KINCAID, C. A. WAY, AND J. O. WOODROW, JR. 1979b. Daily movement patterns of Sigmodon hispidus. Southwestern Naturalist 24:63–69.

CAMERON, G. N., AND S. R. SPENCER. 1985. Assessment of space-use patterns in the hispid cotton rat (Sigmodon hispidus). Oecologia 68:133–139.

CLARK, C. W., AND M. MANGEL. 2000. Dynamic state variable models in ecology. Oxford University Press, New York.

CONNER, L. M., J. C. RUTLEDGE, AND L. L. SMITH. 2010. Effects of mesopredators on nest survival of shrub-nesting birds. Journal of Wildlife Management 74:73–80.

DERRICK, A. M. 2007. Small mammal responses to prescribed fire and simulated mammal removal in a longleaf pine ecosystem. M.S. thesis, University of Georgia, Athens.

DESY, E. A., G. O. BATZLI, AND J. LIU. 1990. Effects of food and predation on behavior of prairie voles: a field experiment. Oikos 58:159–168.

DEUTSCH, J. A., B. O. MOORE, AND S. C. HEINRICHS. 1989. Unlearned specific appetite for protein. Physiology and Behavior 46:619–624.

DICKMAN, C. R. 1992. Predation and habitat shift in the house mouse, Mus domesticus. Ecology 73:313–322.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. 2005. ArcGIS. 9th ed. Environmental Systems Research Institute, Inc., Redlands, California.

FLEHARTY, E. D., AND M. A. MARES. 1973. Habitat preference and spatial relations of Sigmodon hispidus on a remnant prairie in west-central Kansas. Southwestern Naturalist 18:21–29.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

GETTY, T. 1981. Territorial behavior of eastern chipmunks (Tamias striatus): encounter avoidance and spatial time-sharing. Ecology 62:915–921.

GOERTZ, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. Ecological Monographs 34:359–381.

JOULE, J., AND G. N. CAMERON. 1974. Field estimation of demographic parameters: influence of Sigmodon hispidus population structure. Journal of Mammalogy 55:309–318.

KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1994. CALHOME: home range analysis program electronic user's manual. United States Forest Service Pacific Northwest Research Station, La Grande, Oregon.

KINCAID, B. W., AND G. N. CAMERON. 1985. Interactions of cotton rats with a patchy environment: dietary responses and habitat selection. Ecology 66:1769–1783.

LIMA, S. L., AND L. M. DILL. 1989. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

LIU, E. S. 1971. The ethology of the cotton rat, Sigmodon hispidus. M.S. thesis, University of Florida, Gainesville.

MCNAMARA, J. M., AND A. I. HOUSTON. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515–1519.

MORRIS, G. 2010. Effects of mammalian predator exclusion, supplemental feeding, and prescribed fire on small mammal populations in a longleaf pine ecosystem. M.S. thesis, University of Florida, Gainesville.

MORRIS, G., L. M. CONNER, AND M. K. OLI. 2010. Use of supplemental northern bobwhite (Colinus virginianus) food by non-target species. Florida Field Naturalist 38:99–105.

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.

RANDOLPH, J. C., G. N. CAMERON, AND P. A. MCCLURE. 1995. Nutritional requirements for reproduction in the hispid cotton rat, Sigmodon hispidus. Journal of Mammalogy 76:1113–1126.

SAS INSTITUTE INC. 2004. SAS/STAT user's guide, version 9.1. SAS Institute Inc., Cary, North Carolina.

SCHABENBERGER, O., AND F. J. PIERCE. 2002. Contemporary statistical models for the plant and soil sciences. CRC Press, New York.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel estimates for home range analysis. Ecology 77:2075–2085.

SINCLAIR, A. R. E., AND P. ARCESE. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology 76:882–891.

SUMMERLIN, C. T., AND J. L. WOLFE. 1973. Social influences on trap response of the cotton rat, Sigmodon hispidus. Ecology 54:1156–1159.

SWIHART, R. K., AND N. A. SLADE. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019–1025.

SWIHART, R. K., AND N. A. SLADE. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176–1184.

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.

WHITAKER, J. O., JR., AND W. J. HAMILTON, JR. 1998. Mammals of the eastern United States. 3rd ed. Cornell University Press, Ithaca, New York.

WIEGERT, R. G. 1972. Avian versus mammalian predation on a population of cotton rats. Journal of Wildlife Management 36:1322–1327.

YUNGER, J. A. 2004. Movement and spatial organization of small mammals following vertebrate predator exclusions. Oecologia 139:647–651.