SOURCES, SINKS, AND SPATIAL ECOLOGY OF COTTON MICE IN LONGLEAF PINE STANDS UNDERGOING RESTORATION

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The Fire and Fire Surrogate study—a replicated, manipulative experiment—sought the most economically and ecologically efficient way to restore the nation's fire-maintained ecosystems. As part of this study, we conducted a 3-year mark–recapture study, comprising 105,000 trap-nights, to assess demographic responses of cotton mice (*Peromyscus gossypinus*) to Fire and Fire Surrogate treatments at the Gulf Coastal Plain site, where longleaf pine was the ecosystem to be restored. We compared competing models to evaluate restoration effects on variation in apparent survival and recruitment over time, space, and treatment, and incorporated measures of available source habitat for cotton mice with reverse-time modeling to infer immigration from outside the study area. The top-ranked survival model contained only variation over time, but the closely ranked 2nd and 3rd models included variation over space and treatment, respectively. The top 4 recruitment models all included effects for availability of source habitat and treatments. Burning appeared to degrade habitat quality for cotton mice, showing demographic characteristics of a sink, but treatments combining fire with thinning of trees or application of herbicide to the understory appeared to improve habitat quality, possibly creating sources. Bottomland hardwoods outside the study also acted as sources by providing immigrants to experimental units. Models suggested that population dynamics operated over multiple spatial scales. Treatments applied to 15-ha stands probably only caused local variation in vital rates within the larger population.

Key words: cotton mouse, fire, longleaf pine, *Peromyscus gossypinus*, recruitment, reverse time, robust design, source–sink dynamics, survival

The national Fire and Fire Surrogate study was designed to determine the most ecologically and economically efficient methods to reduce fuel loads and restore the nation's fire-maintained ecosystems. Each study site in the Fire and Fire Surrogate network implemented the same 4 treatments representing options for forest restoration: control—no action was taken; burn—prescribed fire was used to reduce fuel levels; thin—trees were removed to reduce tree density; and thin and burn—thinning was followed by prescribed fire. At the Gulf Coastal Plain site of the Fire and Fire Surrogate study, where longleaf pine (*Pinus palustris*) savanna, a critically endangered ecosystem (Noss et al. 1995), was the fire-maintained ecosystem to be restored, a 5th treatment was

added to the 4 Fire and Fire Surrogate treatments: herbicide and burn—herbicide was applied to the shrubby understory followed by prescribed fire.

We examined the effects of time, space, and treatment on the population dynamics of cotton mice (*Peromyscus gossypinus*) for the 3-year span of the study via mark–recapture. We focused on the cotton mouse as a study subject because the species was present in all 15 experimental units, was readily captured, and was present in large enough numbers to estimate demographic variables with confidence. We also chose the cotton mouse because its reported optimal habitat is bottomland hardwood forests, swamps, and mesic or hydric hammocks (hereafter, bottomland hardwoods—Wolfe and Linzey 1977), which we could easily map as potential source habitat (Pulliam 1988) for incorporation into our demographic analysis.

We expected that treatments would create local differences in habitat quality, affecting both fitness within experimental

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units and dispersal of cotton mice between experimental units. We also expected that distance from source habitat, unaffected by our treatments, would affect cotton mouse dispersal. Two traditional theories describe dispersal of animals in a landscape of heterogeneous habitat quality: the ideal free distribution of Fretwell and Lucas (1970) predicts that balanced dispersal (Doncaster et al. 1997) will equalize fitness among habitats, whereas the ideal despotic distribution of Pulliam and Danielson (1991) predicts that source–sink dynamics will cause fitness to differ between habitats. More recently Morris et al. (2004) proposed a theory of reciprocating dispersal whereby the direction of dispersal reverses as the greater population grows or shrinks. Reciprocating dispersal occurs on a short (e.g., seasonal) temporal scale, whereas balanced dispersal or source–sink dynamics are defined over longer periods of time (i.e., generations—Dias 1996; Doncaster et al. 1997; Morris et al. 2004). In a temporal hierarchy, reciprocating dispersal occurs at a level below that of balanced dispersal or source–sink dynamics and can occur as a subprocess within either of the 2 broader processes.

Cotton mice and the longleaf pine ecosystem have several characteristics defined by Van Horne (1983) as prerequisite for source–sink dynamics to develop (e.g., high reproductive rate, habitat generalism, and unpredictable habitat quality over time), but identifying source–sink dynamics is empirically difficult (Dias 1996; Runge et al. 2006). Unequivocal demonstration of a source–sink system requires quantifying emigration, reproduction, and true survival (Runge et al. 2006). Substantiating but less conclusive evidence can be gathered from abundance, population growth rate, apparent survival rates, recruitment rates, age class ratios, and measures of animal health (Runge et al. 2006). Accurately identifying source–sink dynamics also requires long-term investigations that span several generations of the study species (Dias 1996; Morris et al. 2004).

Fire in the southeastern United States affects vegetation in several ways that should benefit cotton mice, which are omnivores and habitat generalists. Soft mast and seed production increase after fire (Van Lear and Harlow 2000), grasses and forbs expand coverage of the forest floor (Brockway and Outcalt 2000), and resprouting vegetation is more nutritious and palatable than older vegetation it replaced (Stransky and Harlow 1981). Three studies of fire in southern pinelands demonstrated an increase in the number of cotton mice captured after fire (Hatchell 1964; Layne 1974; Shadowen 1963). Layne (1974) suggested that the rapid increase in the density of cotton mice was the result of immigration, caused either by overcrowding in areas adjacent to the burn or an increased availability of food on the burned area. Other studies have examined the relationship between cotton mice and microhabitat (Loeb 1999; McCay 2000; Mengak and Guyn 2003), whereas we did not attempt to relate changes in the population to specific microhabitat variables. Our interest was in the overall effect of the treatment.

We hypothesized that the burn, thin–burn, and herbicide–burn treatments would improve habitat for cotton mice by increasing local availability of resources, with the thin–burn treatment causing the greatest improvement. We hypothesized that the thin treatment alone would not affect components of the habitat that are important to cotton mice; therefore, the habitat quality of thin units would be similar to that of control units. Because they are generalists, we hypothesized that cotton mice would be able to obtain adequate resources on thin and control units to survive and reproduce at rates that would maintain population size. We also hypothesized that bottom-land hardwoods in close proximity to experimental units would serve as sources, providing immigrants to those units and obscuring the effects of treatments on population size.

Based on our hypotheses, we predicted that population growth, apparent survival, and recruitment would be highest on thin–burn units, followed by burn and herbicide–burn units; that population growth, apparent survival, and recruitment on thin units would differ little from that of control units, and abundance on thin and control units would not change dramatically from the beginning to the end of the experiment; and that recruitment would be higher in populations close to large areas of bottomland hardwoods and swamps.

MATERIALS AND METHODS

Study area.—The study took place at Auburn University's Solon Dixon Forestry Education Center (Dixon Center), which includes 2,130 ha of managed pine upland and hardwood bottomlands. The Dixon Center is located in Covington and Escambia counties in the Gulf Coastal Plain of south-central Alabama (31.118°N, 86.660°W). Sites selected for experimental units were upland longleaf pine stands in which the natural process of fire had been interrupted; hardwoods had grown into the canopy alongside the dominate longleaf pine. At the time of selection, stands had a dense shrub understory dominated by yaupon (*Ilex vomitoria*) along with lesser amounts of blueberries (*Vaccinium*) and gallberry (*I. glabra*).

Experimental design.—The experiment was a randomized block design, with 3 replicates per treatment. Blocks included 5 experimental units sharing similar soil types and the same general location. All 15 experimental units were forest stands approximately 15.2 ha in size, as specified by the Fire and Fire Surrogate study plan.

Our trapping followed Pollock's (1982) robust design. We conducted 10 trapping sessions (primary periods), each comprising 7 consecutive nights of trapping (secondary periods). Generally, we trapped on each experimental unit twice during the summer of 2001 before application of treatments in the spring of 2002, and twice during each of the 3 summers after application of treatments. Herbicide was not applied until the fall of 2002, followed by burning in the spring of 2003, making the herbicide–burn treatment effectively 1 year behind the others. We trapped each unit once during the winter of 2003 and 2004 to gather more demographic data during the breeding season (Pournelle 1952).

Small mammal trapping.—We sampled the small mammal community using standard mark–recapture methods. We

installed a 0.81-ha trapping grid on each unit. The minimum distance between trapping grids was 156 m. Each grid had 100 trapping stations, each located at the intersection of 10 rows and 10 columns placed at 10-m intervals. We placed a single, large (7.6 × 8.9 × 22.9 cm) Sherman live trap (H. B. Sherman Traps, Inc., Tallahassee, Florida), baited with sunflower seeds, at each trap station. We checked traps each morning. We marked individuals with a uniquely numbered ear tag (number 1 Monel ear tags; Western Tag Co., Salt Lake City, Utah). For each capture we recorded the animal's identification number and standard morphometric data. We determined age based on pelage (Pournelle 1952). Our capture and handling procedures were approved by Auburn University's Institutional Animal Care and Use Committee (PRN 0405-R-2419) and met guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Survival models.—We used the robust design (Kendall et al. 1995, 1997) model in program MARK (White and Burnham 1999) to examine the temporal and spatial structure of apparent survival, the probability that an animal remains alive and available for capture, and to evaluate the effects of the treatments on apparent survival. We treated each of the 15 experimental units as a separate group to build models in program MARK.

To determine the temporal structure of survival that best described the data, we fit models that estimated apparent survival rates seasonally and periodically. For seasonal structure (season), we defined the intervals between primary periods as spring, summer, or fall–winter, according to the time of year between primary periods, and calculated 1 estimate of apparent survival for each of the 3 seasons. For periodic survival (period), we estimated a unique, 30-day, apparent survival rate for each of the 9 intervals between primary periods. We also included a null model, where survival did not vary over time.

To determine the spatial structure of survival that best described the data, we fit models that estimated apparent survival on 4 spatial scales. First, to model the population as continuous across the study area, we included models with no spatial variation in apparent survival estimates. Second, we grouped the 15 experimental units into 5 panmictic neighborhoods (neighborhood), based upon the greatest reported distance dispersed by a cotton mouse, 853 m (Wolfe and Linzey 1977; Fig. 1). To define each neighborhood, we used ArcGIS 8.3 (ESRI 2004) to place a 900-m buffer around each trapping grid and dissolved these buffers into one another at points where they intersected. Third, considering that animals may not disperse the maximum distance, we created a model (locale) representing an intermediate scale between the neighborhood model and the 4th model (unit) with which we assumed each experimental unit hosts a distinct population. We allowed apparent survival rates to vary between experimental units with an effect term for each unit.

We modeled treatments in 3 ways: we considered each treatment a separate effect on apparent survival (treatment); we constrained apparent survival rates on thin units to be equal to those of control units, whereas the 3 other treatments were distinguished (thin = control); and we constrained all units that were burned to have equal apparent survival rates, whereas apparent survival rates on thin units were equal to those of control units (burn). For all treatment models, we constrained estimates of apparent survival to be equal across all units for the pretreatment trapping periods.

We added each of the 4 parameterizations of space and each of the 3 parameterizations of treatment effects to the period, season, and null construction of time. We also constructed models that included only temporal variation in survival. We presumed that treatments caused differential survival between adjacent units, so we did not add terms grouping units in space to treatment models. The only spatial term we included in treatment models was the individual unit term. By including this term we presumed there was within-treatment variation between the 3 replicates. We allowed 1 interactive model (period × burn). These combinations of time, space, and treatment in model structure constituted our a priori set of 30 candidate models. Because these models represent a priori hypotheses explaining biological processes and because the number of explanatory variables is small relative to our sample size, 30 candidate models are reasonable (Burnham and Anderson 2002).

Because our interest was in identifying sources of variation in survival, we did not try to find the most-parsimonious model of capture probabilities, but constructed a model that broadly allowed for potential sources of variation in these estimates. Because the average home range of a cotton mouse is 0.5 ha and the average life span is ≤5 months (Wolfe and Linzey 1977), we assumed the probability of temporary emigration (Kendall et al. 1997) to be 0. We used the Huggins closed capture estimator (Huggins 1989, 1991) to calculate capture probabilities and derive estimates of abundance. Heterogeneity in trappability between individuals can cause bias in capture and recapture estimates (Otis et al. 1978). We used individual covariates in the Huggins estimator to account for differences in trappability between individuals caused by age, sex, and a behavioral response to trapping within and between primary periods. Because of computational limitations caused by the size of our data set, we calculated only 1 probability of capture and 1 probability of recapture for each unit for each primary period. A general, time varying model of capture probabilities such as this is appropriate for estimating population size (Burnham and Anderson 2002).

Because of the size of our data set, the use of individual covariates in program MARK would have greatly protracted model analysis. Therefore, we adopted a 2-step model selection process. First, we ran the a priori set of candidate models of survival without any individual covariates. From these models we chose the model with the lowest Akaike information criterion adjusted for small sample size (AIC_c—Akaike 1973; Hurvich and Tsai 1989) and all models that differed from that model in AIC_c value (ΔAIC_c) by ≤7; added age as a covariate with survival; added age, sex, and previous capture history as covariates with capture probabilities; and reran the models.

$\Delta AIC_c \leq 7$ is a conservative cutoff point (Burnham and Anderson 2002), insuring that the best approximating model was included in the 2nd generation of models. We drew conclusions from the results of this 2nd generation of models.

Recruitment models.—We performed a reverse-time survival analysis to analyze recruitment to the population through births and immigration (Pradel 1996). The reverse-time equivalent to survival is seniority, the probability an animal was in the population at time $i - 1$, given it was in the population at time i. Recruitment is equal to $1 -$ seniority. We followed the example of Nichols et al. (2000), using multistate modeling to separate age classes into 2 states: adults and subadults. The robust design multistate models in program MARK integrate multistate modeling developed by Brownie et al. (1993) and Hestbeck et al. (1991) with the full likelihood robust design model of Kendall et al. (1995). If the probability of recapturing an animal differs from the probability of initially capturing the animal (model M_b—Otis et al. 1978), capture histories that are not palindromic have different models of probability if read in reverse (see Williams et al. 2002:table 14.1). To ensure that we estimated the correct capture probabilities, we retained the forward time order of the secondary periods and only reversed the order of the primary periods.

Models of recruitment resembled the survival models. We used only the period time structure (the best structure of time for survival). We used the closed robust design multistate model, which removes temporary emigration from the likelihood.

Because subadults could not have been in the population during the previous primary period, we set the seniority probability for subadults to be 0. Breeding subsides in the summer and so captures of subadults were low during those primary periods. To facilitate calculations for periods when data were sparse, we constrained subadult capture and recapture probabilities to be equal for all July primary periods and June of 2004. We estimated separate transition probabilities for each of the spring intervals; all other intervals were constrained to have the same estimate for transition probability.

We implemented treatment effects on seniority in the same manner we did with survival models. To evaluate whether bottomland hardwoods were sources of immigrants to experimental units, we incorporated unit-specific measures of bottomland hardwoods as covariates. We used ArcGIS 8.3 (ESRI 2004) to map the 15 trapping grids and all bottomland hardwoods within the study area (Fig. 1). We placed a 900-m buffer around each trapping grid to represent the furthest distance from which a cotton mouse was likely to have immigrated onto the grid. Within each buffer we summed the total area of bottomland hardwoods and calculated the mean distance to the trapping grid from all map cells containing bottomland hardwoods. For entry into program MARK, we standardized these values.

We used AIC_c (Akaike 1973; Hurvich and Tsai 1989) and the methodology of Burnham and Anderson (2002) for survival and recruitment model selection and inference.
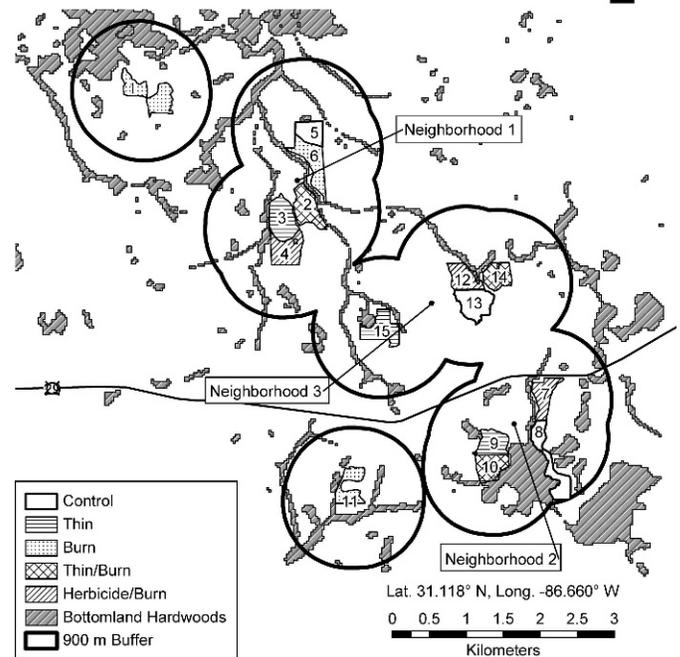
FIG. 1.—Map of the Fire and Fire Surrogate Study's Gulf Coastal Plain experimental design, showing numbered experimental units with treatment applied and 900-m buffers for spatial segregation of neighborhoods and quantification of bottomland hardwoods.

Population size and growth.—To evaluate treatment effects on population growth rate, we calculated a time-averaged rate for each experimental unit (λ—Caswell 2001) for the 3-year span of the study, our time frame of interest, using:

$$\lambda = e^{\frac{(\log N_t - \log N_0)}{t}},$$

where t is 3 (time span of 3 years); N_t is population size from the last period of the study (period 10); and N_0 is the population size at the same time of year as period 10, 3 years previous, before treatment (period 2). We took estimates of population size from the selected best model of survival from program MARK. We used the delta method (Seber 2002) to estimate the variance of λ, for construction of 95% confidence intervals (95% CIs):

$$\widehat{var}\left(\hat{\lambda}\right) = \left(\frac{\partial \hat{\lambda}}{\partial \hat{N}_i}\right) \cdot \hat{\Sigma} \cdot \left(\frac{\partial \hat{\lambda}}{\partial \hat{N}_i}\right)^T,$$

where $\hat{\Sigma}$ is the variance–covariance matrix of $\hat{N}_i$ produced by program MARK.

RESULTS

Over 105,000 trap-nights we captured 1,190 cotton mice 5,027 times.

Survival models.—Seven of the original 30 models had a $\Delta AIC_c \leq 7$ and were revised with individual covariates (Table 1). All of these structured survival periodically with regard to time. Virtually no support existed for structuring survival seasonally (0.009 summed weight for all seasonal

TABLE 1.—Summary of model selection results for apparent survival of cotton mice (*Peromyscus gossypinus*) in Covington and Escambia counties, Alabama, 2001–2004. Models are ranked in ascending order by Akaike's information criterion, adjusted for small sample size (AIC_c). Top models all estimated a unique apparent survival rate for each of 9 intervals between trapping periods (period). Neighborhood and locale represent 2 spatial aggregations of experimental units. The neighborhood configuration was constructed by placing 900-m buffers around experimental units, whereas the locale configuration was constructed with a maximum 570-m buffer. Treatments were modeled in 1 of 3 ways: each treatment—thin, burn, thin–burn, herbicide–burn, and control—was estimated to have unique effect (treatment); thin units were estimated to have the same estimates of apparent survival as control units, and all other treatments had a unique effect (thin = control); or all units that were burned were constrained to have the same estimate of apparent survival, and thin units were constrained to have the same estimates of apparent survival as control units (burn).

Model	AIC_c	ΔAIC_c	AIC_c weight	K[a]	Deviance	Evidence ratio[b]	Cumulative weights[c]
Period	17,496.15	0.00	0.56	150	17,186.76		0.56
Period + neighborhood	17,498.14	1.99	0.21	154	17,180.23	2.70	0.76
Period + thin = control	17,498.63	2.48	0.16	153	17,182.86	3.46	0.92
Period + treatment	17,500.85	4.70	0.05	154	17,182.95	10.50	0.97
Period + locale	17,502.72	6.57	0.02	155	17,182.69	26.75	1.00
Period × burn	17,505.62	9.47	0.00	157	17,181.32	114.14	1.00
Period + burn	17,539.27	43.12	0.00	151	17,227.75	2.31×10^9	1.00

[a] Number of parameters.
[b] Likelihood of the top-ranked model versus the competing model (e.g., the top model is 2.7 times more likely to be the model that best approximates truth than the 2nd ranked model).
[c] Sum of the AIC_c weights from the competing model and each higher ranked model.

models) or without a time effect (0.007 summed weight for all time-invariant models).

The top 3 survival models were viable explanations for the data ($\Delta AIC_c < 3$—Burnham and Anderson 2002) with 92% of the AIC_c weight (Table 1). The period model ranked highest, allowing survival to vary for each interval between primary periods but not spatially or by treatment (Table 1). The 2nd best model, period + neighborhood, added the 900 m spatial configuration and the 3rd best model, period + thin = control, added a treatment effect with the thin treatment being equal to the control. Evidence ratios suggested models period + neighborhood and period + thin = control compared favorably with model period (Table 1). Following guidelines suggested by Burnham and Anderson (2002), model period + neighborhood and model period + thin = control had strong and moderate support, respectively, for consideration as the best approximating model, given uncertainty in the information criterion. Other models had little support.

Estimates of monthly adult apparent survival rates from the top model, period, ranged from 0.57 (95% *CI* = 0.47, 0.66) to 0.80 (95% *CI* = 0.75, 0.84). *CI*s for all treatment and spatial effects included 0, making apparent survival estimates within and between models statistically indistinguishable. Still, treatment and spatial terms held information, indicated by competitive model AIC_c values and decreased deviances (Table 1; Burnham and Anderson 2002), revealing trends in the data useful for evaluating hypotheses. Model period + neighborhood suggested that neighborhood 1 had the highest apparent survival rates, followed by neighborhood 3, neighborhood 2, unit 1, and finally unit 11. Units 1 and 11 were burn units. Model period + thin = control suggested that apparent survival is lower on burn units and higher on thin–burn and herbicide–burn units, relative to the thin and control units.

Recruitment models.—The top 4 models were all viable explanations for the data ($\Delta AIC_c < 3$—Burnham and

Anderson 2002) with 77% of the AIC_c weight (Table 2). Evidence ratios showed that the 2nd, 3rd, and 4th ranked models compared favorably with the top model. All of the top 4 models contained effects for total area of source habitat within 900 m, average distance to source habitat within 900 m, and effects for either treatment or equating thin units to control units. The AIC rankings indicated equating thin units to control units was a more parsimonious characterization of treatment effects than handling thin units separately (Table 2).

Seniority rates were high. Estimates from the top-ranked model ranged from 0.55 (95% *CI* = 0.42, 0.67) to 0.99 (95% *CI* could not be calculated because the estimate was near the upper maximum-likelihood boundary). Area of source habitat had a negative monthly effect of 0.96% on seniority (β_{area} = −0.17, 95% *CI* = −0.31, −0.03). Average distance to source habitat had a positive monthly effect of 0.82% on seniority ($\beta_{avg\ dist}$ = 0.17, 95% *CI* = 0.02, 0.32). The effect of burning on seniority was a 3.39% monthly decline (β_{burn} = −0.51, 95% *CI* = −0.87, −0.16). Other treatment effects were statistically indistinguishable from the controls. Regardless, model selection indicated that the model terms for these treatments contain valuable information about recruitment (1 − seniority). The top 2 models (with the thin = control parameterization) indicated that recruitment was highest on burn units, followed by herbicide–burn units, thin and control units, and finally thin–burn units. The 3rd and 4th ranked models (with the treatment parameterization) indicate the same order except units with the thin treatment had higher recruitment than control units.

Population size and growth.—Abundance estimates per trapping grid, from model period, ranged from 1.22 (95% *CI* = 1.01, 5.65) to 63.30 (95% *CI* = 13.97, 383.9). Burn units had the highest observed rate of population growth for the 3-year span of the study (Fig. 2). Control units had the lowest growth rates, showing declining populations. Thin–burn units

TABLE 2.—Model selection results for recruitment of cotton mice (*Peromyscus gossypinus*) in Covington and Escambia counties, Alabama, 2001–2004. Models are ranked in ascending order by Akaike's information criterion, adjusted for small sample size (AIC$_c$). Treatments were modeled in 1 of 3 ways: each treatment—thin, burn, thin–burn, herbicide–burn, and control—was estimated to have unique effect (treatment); thin units were estimated to have the same estimates of apparent survival as control units, and all other treatments had a unique effect (thin = control); or all units that were burned were constrained to have the same estimate of apparent survival, and thin units were constrained to have the same estimates of apparent survival as control units (burn). Area = total area of bottomland hardwoods within 900 m of each experimental unit. Avg dist = average distance to all 30-m map cells containing bottomland hardwoods within 900 m of each experimental unit.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	K[a]	Deviance	Evidence ratio[b]	Cumulative weights[c]
Area + avg dist + thin = control	17,787.17	0.00	0.33	64	17,657.50		0.33
Area × avg dist + thin = control	17,788.10	0.92	0.21	65	17,656.37	1.59	0.54
Area + avg dist + treatment	17,788.91	1.74	0.14	65	17,657.18	2.38	0.68
Area × avg dist + treatment	17,789.89	2.72	0.09	66	17,656.11	3.90	0.77
Avg dist + thin = control	17,790.92	3.75	0.05	63	17,663.30	6.52	0.82
Area × avg dist	17,791.77	4.59	0.03	60	17,670.29	9.94	0.85
Thin = control	17,791.87	4.69	0.03	62	17,666.29	10.46	0.88
Area × avg dist	17,792.25	5.08	0.03	62	17,666.68	12.67	0.91
Avg dist + treatment	17,792.86	5.68	0.02	64	17,663.18	17.15	0.93
Period × burn	17,793.51	6.33	0.01	61	17,669.98	23.73	0.94
Treatment	17,793.61	6.44	0.01	63	17,665.99	25.00	0.96

[a] Number of parameters.

[b] Likelihood of the top-ranked model versus the competing model (e.g., the top model is 1.59 times more likely to be the model that best approximates truth than the 2nd ranked model).

[c] Sum of the AIC$_c$ weights from the competing model and each higher ranked model.

showed stable or slightly declining growth rates. Thin units and herbicide–burn units showed both declining and increasing growth rates (Fig. 2).

DISCUSSION

Our goal was to evaluate the spatiotemporal response of cotton mouse population dynamics to alternative approaches to restoring the fire-maintained longleaf pine ecosystem. Using a replicated, manipulative experiment, intense mark–recapture sampling, and robust modeling, we found evidence for source–sink dynamics in cotton mouse populations, inferred emigration from bottomland hardwoods to support

FIG. 2.—Population growth rates, with 95% confidence intervals, for a 3-year span from 2001 to 2004, ranked in descending order, for populations of cotton mice (*Peromyscus gossypinus*) living on experimental units treated for habitat restoration, in Covington and Escambia counties, Alabama.

the hypothesis these habitats are sources of cotton mice, and suggest that population dynamics operated over multiple spatial scales.

Effects of restoration treatments.—Our models indicated that treatments designed to restore fire effects on longleaf pine stands had modest effects on apparent survival but important effects on recruitment. The top-ranked survival model included no variation by treatment in apparent survival estimates. The thin = control parameterization of survival ranked 3rd and estimated treatment effects included 0 in the 95% CI. This implies that variation in apparent survival rates between treatments was relatively small, but even small differences in survival between treatments could cause noticeable changes in the population growth rate, as evidenced by high seniority estimates (Nichols et al. 2000). Conversely, there was enough variation in recruitment between treatments that treatment models performed strongly in the recruitment analysis and 0 was not included in the estimate of the 95% CI for the effect of the burn treatment.

Our hypothesis that thinning would not alter habitat in a way that affects cotton mice and that habitat quality on thin sites was similar to that of controls was supported. Survival and recruitment models that equated thin and control units outperformed models that treated them differently. Our results do not support the hypothesis that cotton mice living on thin and control units would be able to obtain adequate resources to survive and reproduce at rates that maintain the size of the population. All of the control units and 1 thin unit had population growth rates much lower than 1 (Fig. 2), suggesting that habitat quality on these units was poor (Van Horne 1983). We hypothesize that exclusion of fire in these stands resulted in a dense shrub layer that shaded out grasses and forbs resulting in the loss of important foods, or that leaf litter became so deep that it was difficult for mice to forage for food.
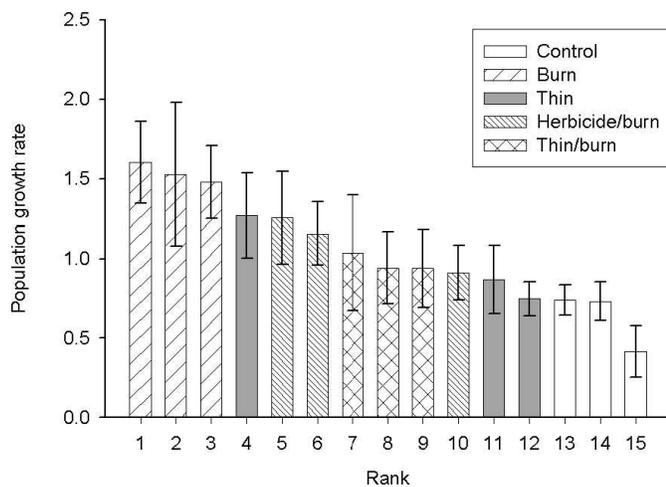
We hypothesized that burning would improve habitat quality for cotton mice by increasing local availability of resources, with the thin–burn treatment causing the best improvement. This hypothesis had mixed support. Thin–burn units had population growth rates close to 1 and the highest apparent survival rates, but the lowest recruitment rates— lower than that for the controls (Fig. 2). A source is expected to have a stationary population growth rate over several generations (=1) as resident individuals live long (high survival) and only enough individuals are recruited to the population to replace those that die (low recruitment); excess individuals are exported (Pulliam 1988).

The herbicide–burn treatment also appears to have improved habitat for cotton mice. Two of these sites had population growth rate estimates greater than 1, although 1 is included in the estimated 95% *CI*s for all 3 herbicide–burn units (Fig. 2). The herbicide–burn units had the 2nd highest apparent survival rates and recruitment rates, improved over control units.

Unlike the thin–burn treatment, the burn treatment appears to have decreased habitat quality below that of the control units. These units had population growth rates much higher than 1 and the highest recruitment rates, but apparent survival rates lower than the controls. These rates are characteristic of a sink wherein turnover of individuals is high (Pulliam 1988) or pseudosinks wherein high densities caused by immigration depress habitat quality (Watkinson and Sutherland 1995). A newly created sink or pseudosink could exhibit a rapidly growing population as animals displaced from sources spill into the area (Pulliam 1988). We could not explicitly calculate immigration from outside the study area as did Nichols et al. (2000), because we could not determine whether mice were born within or outside experimental units. Because the top 4 recruitment models all included measures of source habitat outside the experimental units, however, we hypothesize that increased immigration rates were primarily responsible for population growth in these stands rather than increased reproduction. If true, this hypothesis argues for effects of burning that vary depending on whether it is combined with other means of reducing density of over- and midstory plants. Anecdotally, we noted that the thin–burn and herbicide–burn treatments appeared more effective in reducing light competition for understory plants, facilitating the beneficial effects of fire to cotton mouse habitat (e.g., increased production of edible herbs, seeds, and fruit). We therefore hypothesize that burning alone decreases habitat quality for cotton mice, creating a sink, but burning combined with thinning or herbicides increases habitat quality, creating a source.

Alternatively, our results could be interpreted to suggest that the burn treatment improved habitat quality and did not create sinks, but sources. The high growth rate could be indicative of a population growing to a higher carrying capacity, and the high recruitment rate could reflect a high birth rate. The low apparent survival rate could reflect a high rate of emigration as surplus production disperses. We cannot state definitively that this interpretation of the data is

incorrect. As Runge et al. (2006) point out, the definitive factor would be some estimation of emigration from each habitat, but this requires quantifying birth rates and some way to resight individuals that move to different habitats, both of which are difficult to do with mice. Nonetheless, we find it difficult to explain how the thin–burn treatment and the burn treatment could both have improved habitat, possibly creating sources, given that the 2 treatments show exactly opposite effects on apparent survival and recruitment.

Source habitat effects.—Our results provide circumstantial support for the hypothesis that bottomland hardwood forests and swamps are high-quality habitat for cotton mice that serve as sources (Wolfe and Linzey 1977). Our hypothesis that bottomland hardwoods close to experimental units would provide immigrants to those units was supported by our data. Recruitment increased with an increase in the total area of bottomland hardwoods within 900 m and decreased as the average distance to bottomland hardwoods within 900 m increased. Because recruitment includes births and immigration and it is unlikely bottomland hardwoods outside the study area increased the birth rates of mice living within the study area, we thus infer that this habitat was a source of immigrants into our experimental units.

The difference in immigration between experimental units caused by availability of source habitat did not obscure treatment effects on population growth, contrary to our hypothesis. By ranking units in descending order of population growth rate, a clear pattern of treatment effect emerged (Fig. 2). The 3 burn units had the highest growth rates, 2 of 3 herbicide–burn units had the 2nd highest rates, thin–burn units had stable (or nearly stable) rates, 2 of 3 thin units had the 2nd lowest rates, and control sites had the lowest rates. The strong contribution to population growth rate by survival apparently overshadowed differences in recruitment between units caused by immigration from source habitat. The pattern was not perfect because 1 herbicide–burn unit and 1 thin unit were not in the expected order. Neither these departures from expected order, nor the rankings of experimental units within treatments, were explained by availability of source habitat.

The rank of experimental units by population growth rate within the thin–burn, thin, and control treatments was best explained by the period + neighborhood survival model, indicating that it is important to consider the spatial extent over which vital rates are operant within a population. In our case this spatial extent was best explained by dispersal distance, further evidence of the strong role played by source–sink dynamics in the population we studied. Strong evidence for our survival and recruitment models based on the maximum dispersal distance of cotton mice supports the suggestion of Danielson and Anderson (1999:100) that dispersal capabilities may play an important role ''in determining the spatial extent of a species' landscape.'' Our models suggest that the functional spatial extent of the cotton mouse populations we studied might be ≥900 m, contrary to the abundance-based estimate of ≤300 m of Danielson and Anderson (1999). We hypothesize that differences in habitat quality between the 2

study locations did not account for this disparity because cotton mice are habitat generalists that move relatively unhindered through various patches of habitat quality in a fragmented landscape (Danielson and Anderson 1999; Mabry et al. 2003). The difference may be due to our use of dispersal distance to delineate the population, which might be a better measure of a species' ability to exploit available habitat than abundance (Danielson and Anderson 1999).

Habitat quality and spatial scale.—Defining habitat quality requires delimiting the spatial extent of the habitat and linking vital rates to the delimited area (Garshelis 2000). These 2 objectives are often ignored in empirical studies of habitat quality, where vital rates are rarely measured and habitat extent is usually defined arbitrarily. We defined spatial extent of habitat in our neighborhood model to reflect likely panmictic cotton mouse populations. We hypothesized that mice within these populations shared a similar ability to exploit the particular resources available within the neighborhood, so constraining vital rate estimation to the panmictic population should yield a more accurate reflection of habitat quality. Similarly, we based the spatial extent of habitat in our recruitment models on the maximum dispersal distance of cotton mice, allowing us to identify source habitats likely to influence recruitment. Because we identified spatial extent of the habitat we studied based on cotton mouse biology and linked it directly to the estimation of vital rates, our conclusions about habitat quality are particularly robust.

Because the size of the experimental units in our study was chosen without regard for the biology of cotton mice, we cannot conclude that the treatments applied to 15-ha stands were sufficient to substantially affect the population; rather, they most likely caused local variation in vital rates within the larger population. We hypothesize that this is because the size of our experimental units was likely smaller than the spatial scales over which variation in vital rates can have population-level effects for cotton mice. This interpretation explains how 2 survival models, 1 suggesting no spatial heterogeneity in the cotton mouse population and the other finding treatment effects on mice living within small experimental units, could both rank as plausible explanations under AIC and yet estimates of treatment effects were statistically insignificant. This interpretation would not have been apparent, had we not evaluated models competing over different spatial scales.

ACKNOWLEDGMENTS

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