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# Habitat associations of the marsh rice rat (*Oryzomys palustris*) in freshwater wetlands of southern Illinois

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The marsh rice rat (*Oryzomys palustris*) is a semiaquatic rodent occurring in wetland habitats throughout the southeastern United States and along the Atlantic Coast. A lack of understanding of its ecology and distribution in inland parts of its range limits our ability to assess the species' status and needs. We trapped rice rats at random and previously occupied, wetland-dominated sites in 5 southern Illinois watersheds during 2007–2009 to determine key variables affecting habitat occupancy by the species. We detected rice rats within 3 of 5 watersheds, 16 of 48 sites, and at 5 new locations. Most rice rats were captured in permanent or semipermanent emergent wetlands ($n = 89$; 46.3% of total captures) or roadside ditches in wetland patches ($n = 73$; 38.0%). Habitat associations determined using logistic regression and occupancy modeling provided similar results. Percent herbaceous cover and percent visual obstruction (0.0–0.5 m) were the most important microhabitat variables positively influencing rice rat occurrence. In areas surrounding wetlands, the proportion composed of upland grass was the best predictive variable of rice rat occurrence among landcover models. Estimates of daily detection probability were high (0.44–0.87). The likelihood of occupancy increased with the proportion of upland grass cover adjacent to wetland complex and percent herbaceous cover at the microhabitat scale. Inland metapopulations of rice rats are clustered throughout the southeastern United States in appropriate wetland complexes. Construction, restoration, and protection of emergent wetlands, and consideration of connectivity and adjacent grasslands, should benefit rice rat populations.

Key words:   habitat associations, inland populations, marsh rice rat, occupancy modeling, *Oryzomys palustris*, wetlands

Understanding factors affecting the presence or absence and density of a species helps elucidate habitat selection, predict range expansion or contraction, and model species responses to habitat manipulation or change. Recently, researchers have used occupancy surveys coupled with habitat measurements to assess factors affecting distribution in mammals of conservation concern (*Brachylagus idahoensis* [Larrucea and Brussard 2008] and *Neotoma floridana smalli* [Winchester et al. 2009]).

The marsh rice rat (*Oryzomys palustris*) is a semiaquatic rodent occurring in wetland habitats throughout the southeastern United States and along the Atlantic Coast. Although this species is found in freshwater and saltwater wetlands, studies of its population (Bloch and Rose 2005; Negus et al. 1961; Wolfe 1985) and habitat (Forys and Dueser 1993; Kruchek 2004; Martin et al. 1991) ecology have been conducted primarily in coastal marshes with tidal fluctuations. Found in a variety of primarily herbaceous wetland types, rice rats characteristically are associated with extensive *Spartina*

*alterniflora* marsh in coastal regions (Forys and Dueser 1993; Kruchek 2004; Martin et al. 1991), with hints that freshwater wetlands may be avoided (Martin et al. 1991). The silver rice rat (*O. p. natator*), a federally endangered subspecies (United States Fish and Wildlife Service 2007), uses saltwater habitats almost exclusively and rarely is captured in freshwater wetlands (United States Fish and Wildlife Service 1999). Rice rats forage primarily on aquatic organisms and wetland vegetation and use adjacent upland habitats for refuges during periods of flooding (Kruchek 2004).

The ecology of inland populations of rice rats using freshwater wetlands in the southeastern United States is poorly understood. The species appears to occur at low densities, because most references to rice rats occurring inland

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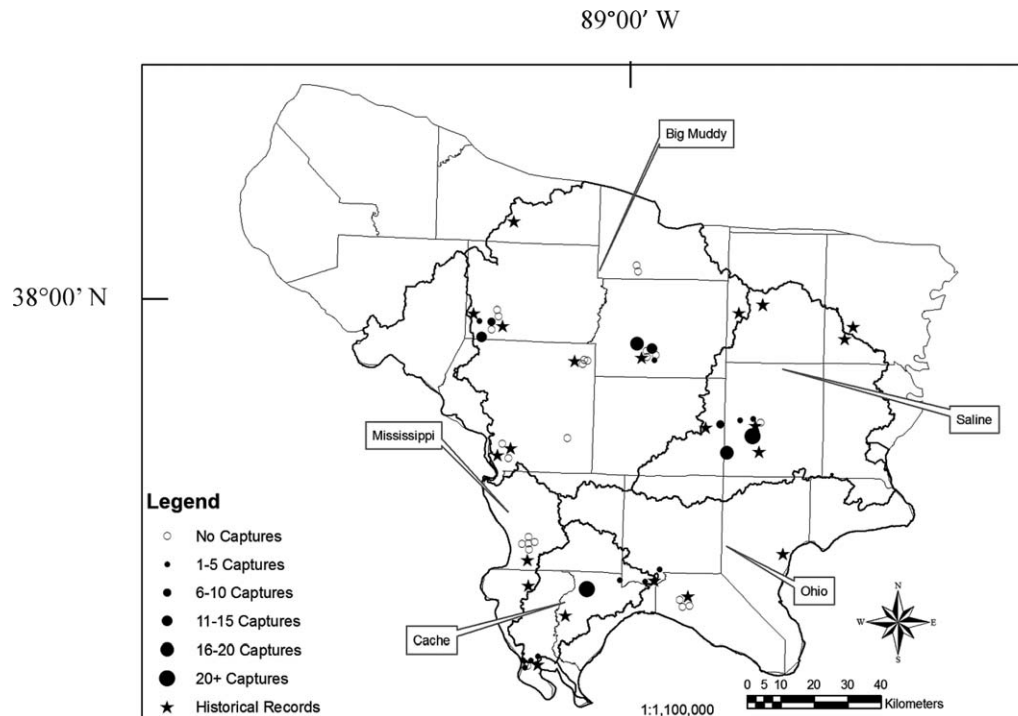
Fig. 1.—Trapping locations and number of marsh rice rat (*Oryzomys palustris*) captures (circles) during survey for marsh rice rats in southern Illinois, 2007–2009. Stars represent historical records. Gray lines represent county borders, and black lines represent watershed boundaries. Sampled watersheds are labeled in boxes.

are suggested anecdotally in studies of small-mammal communities (Constantine et al. 2004; Whitsitt and Tappe 2009). However, they can be locally abundant (12–57 individuals/ha—Chamberlain and Leopold 2003; Smith and Vrieze 1979). In addition, a niche attribute consistent to rice rat habitat across salinity levels is the presence of dense, emergent vegetation, including cattails (*Typha* sp.), sawgrass (*Cladium jamaicense*), and common reed (*Phragmites australis*) in freshwater systems.

The rice rat is currently listed as a state-threatened species (Herkert 1992) in Illinois. Reasons cited for its status include historical wetland loss and the species' existence at the northern edge of its range (Hoffmeister 1989; Wolfe 1982). This status renders the rice rat an important indicator species for wetland habitats and a species of concern in applications for land-use permits (e.g., surface mining). Historically, specimens in Illinois generally were captured in shallow wetlands, including palustrine emergent, palustrine scrub–shrub, palustrine aquatic bed, and riverine aquatic bed (Cowardin et al. 1979; Hofmann et al. 1990). Hofmann et al. (1990) concluded that optimal habitat for the species in southern Illinois included standing water and emergent wetland vegetation. Records ranging from 1975 (Urbanek and Klimstra 1986) to more recent (approximately 2006) unpublished notes (G. A. Feldhamer and T. Carter, Southern Illinois University Carbondale, pers. comm.; C. K. Nielsen, Southern Illinois University Carbondale, pers. comm.) suggest that the species is colonizing moist-soil and emergent wetlands dominated by common reed, including wetlands associated with reclaimed surface mines and within subsi-

dence basins above underground coal mines. Wetland restorations by state, federal, and nongovernmental organizations and an increase in mine-associated wetlands might have provided rice rats with opportunities for dispersal and population expansion in the last 3 decades, as rice rats are effective dispersers over both land and water (Loxterman et al. 1998). Our objectives were to assess the distribution of marsh rice rats in wetland-dominated sites in southern Illinois and to determine key microhabitat and landcover variables affecting habitat occupancy.

## MATERIALS AND METHODS

*Site selection.*—We sampled 29 sites in southern Illinois, centered at approximately 38°00′N and 89°00′W (Fig. 1), where rice rats previously had been documented. In addition, we entered trap-site locations from 1987 Illinois Natural History Survey data files (Hofmann and Gardner 1987) into ArcGIS version 9.2 (Environmental Systems Research Institute 2004) and generated circular 50-ha buffers around trap sites. We used the National Wetlands Inventory (Cowardin et al. 1979) layer to determine wetland types and associated size (ha) surrounding each site. Sites where Hofmann and Gardner (1987) captured rice rats supported an average of 20 ha of wetlands within the 50-ha buffer. We used ArcGIS version 9.2 (Environmental Systems Research Institute 2004) to generate points randomly within each of the 8 major watersheds (Big Muddy, Cache, Embarras, Kaskaskia, Little Wabash, Mississippi, Ohio, Saline, and Wabash) in southern Illinois proportional to total wetland area contained within each watershed.

Once random points were generated, we selected points that fell within a National Wetlands Inventory–designated wetland. We established a 50-ha circular buffer around these remaining points and selected only those that included ≥20 ha of wetlands within this buffer. This process resulted in 183 prospective trapping locations within the major watersheds of southern Illinois. Nineteen of these prospective sites were sampled for marsh rice rats among 5 major watersheds based on accessibility, ownership, and logistical constraints (Fig. 1).

*Livetrapping and density estimation.*—We used 10–100 Sherman collapsible live traps ($8 \times 9 \times 23$ cm; H. B. Sherman Traps Inc., Tallahassee, Florida—Hofmann et al. 1990; Kruchek 2004) per site. We trapped for 5 nights at each site. We conducted trapping sessions between October 2007 and March 2009, because rice rats are considered equally susceptible to trapping throughout the year (Negus et al. 1961). Each site was sampled during a single session except for the West Harrisburg site, which was sampled during 4 sessions at seasonal intervals. When possible, we placed traps in areas with dense herbaceous cover, close proximity (usually <3 m) to standing water, and near logs, runways, or other structures to increase probability of capture. Although trap arrangement (e.g., grids and transects) varied from site to site based on amount and configuration of habitat, we always spaced traps at 10-m intervals. We baited traps with rolled oats, a mixture of peanut butter and rolled oats, or a birdseed mixture. We checked and closed the traps every morning to avoid capturing nontarget species. Closing traps during the day should not have influenced the probability of capture, because rice rats are strictly nocturnal (Negus et al. 1961; Worth 1950). Each afternoon we returned to reset traps and rebait as necessary. During cold-weather trapping, we placed bedding material in each trap to provide insulation for captured animals.

We marked captured individuals with a unique numbered ear tag. We recorded reproductive condition, based on the position of testes for males and perforated vagina, pregnancy, or lactation for females (Hofmann et al. 1990; Kruchek 2004; Negus et al. 1961). We recorded body mass to the nearest gram using a Pesola spring scale (Forestry Supplies, Inc., Jackson, Mississippi). We recorded length measurements of the head, body, tail, ear, and hind foot to the nearest 1 mm. Protocols for capture and handling of rice rats were approved by the Institutional Animal Care and Use Committee at Southern Illinois University Carbondale (protocol 07-009), and followed guidelines of the American Society of Mammalogists (Gannon et al. 2007).

*Habitat measurements.*—We characterized rice rat habitat with microhabitat variables. Microhabitat measurements were taken at a random sample of 10% of trap locations. To avoid analyzing areas that were affected by trapping activities, we placed the quadrat 2 m from the trap location in a random direction. We recorded percentage cover of herbaceous plants (grass and forb), bare ground, shrub, and rock (Snyder and Best 1988) within a square 0.25-m² quadrat. Also, we noted the presence of several common wetland plants—sedges (*Carex* spp.), rushes (*Juncus* spp.), smartweed (*Polygonum*

TABLE 1.—Names and descriptions of landcover classes used to examine habitat factors associated with marsh rice rat (*Oryzomys palustris*) occupancy in southern Illinois, 2007–2009. Wetland codes are based on Cowardin et al. (1979).

| Name | Description |
| --- | --- |
| AG | Active row-crop agricultural land |
| DEV | Roads, buildings, and other developed lands |
| NON_FOR | Sum of all wetland types except for palustrine forested wetlands |
| PEMA | Palustrine emergent wetland intermittently flooded to seasonally inundated |
| PEME | Palustrine emergent wetland at minimum semipermanently to permanently flooded |
| PFO | Palustrine forested wetland |
| PSS | Palustrine shrub–scrub wetland |
| TOT_WET | Sum of all wetland types |
| UP_FOR | Nonwetland forested habitat |
| UP_GRASS | Nonwetland grassland habitat |
| WATER | Permanent lakes, ponds, or rivers |

spp.), cattail (*Typha* spp.), common reed, or buttonbush (*Cephalanthus occidentalis*)—within the quadrat. We calculated the average proportion of quadrats where a species occurred for sites that were occupied and not unoccupied by rice rats and report that as a measure of individual plant-species occurrence.

We placed a cover pole in the center of each quadrat to establish a 5-m circular plot. We measured visual obstruction from each cardinal direction at a distance of 5 m and recorded percentage of visual obstruction at heights of 0.0–0.5 m, 0.51–1.0 m, and 1.01–1.5 m. Woody stem density was measured by walking a 10-m transect with arms outstretched (2 m) and counting the number of woody stems touched. Finally, we recorded the distance to the nearest standing water source from each location by direct field measurement or electronic map measurement (for longer distances).

We used ArcGIS version 9.2 (Environmental Systems Research Institute 2004) to record landcover variables within a 50-ha circular buffer from the center of the trapping grid. The digital National Wetlands Inventory layer for southern Illinois was based on data from 1981 and did not accurately reflect many of the trapping locations because those sites have been influenced recently by human activities such as wetland management or coal mining practices. Therefore, we used satellite imagery (United States Department of Agriculture 2007), digital soil maps (United States Department of Agriculture 2009), and personal knowledge of the site in conjunction with National Wetlands Inventory data to characterize current landcover types within the buffer. Wetland types were classified by vegetation, hydrology, and soil characteristics based on Cowardin et al. (1979). After the original wetland types were classified, we grouped all landcover types into 9 distinct categories (Table 1). Finally, we classified the area within the 50-ha circular buffer into these categories and used the proportion of each landcover class for logistic regression analysis.

We also examined the relationship of mined lands and presence of common reed within 50 m of the trapping grid

(based on satellite imagery) with rice rat occurrence. We classified surface-mine lakes, subsidence basins, and slurry ponds as mine-associated wetlands and classified moist-soil units, reservoirs, and natural wetlands as nonmined wetlands.

*Data analyses.*—The number of captures at any given site was inadequate for formal mark–recapture analyses. Therefore, we developed a minimum density estimate using an ad hoc method. Average home-range size for rice rats in Illinois has been estimated to be 0.73 ha (J. E. Hofmann, Illinois Natural History Survey, pers. comm.). We used ArcMap (Environmental Systems Research Institute 2004) to digitize trapping transects at all sites that had >10 rice rat captures. We created a 96.4-m circular buffer around each transect to represent the average home-range size of a rice rat. This buffer width represents the diameter of a 0.73-ha circle. We divided the number of individual rice rats captured by the area of the buffer to obtain minimum density estimates. Because the distance of transects varied from site to site, we created buffers around individual transects, rather than sites, to reflect densities. We also used chi-square tests of homogeneity to compare the frequency of mine-associated and nonmine-associated wetlands where we captured rice rats, and to examine the association of common reed with site occurrence by rice rats.

We constructed logistic regression models with presence or absence of rice rats on the site as the binary response variable. Microhabitat and landcover variables were used as independent variables. We examined all single-variable models and developed multiple-variable models based on combinations of habitat variables deemed important to rice rat biology (Hofmann et al. 1990). Models were compared using Akaike's information criterion adjusted for small sample size ($AIC_c$), with models considered as competitive if within 2 $AIC_c$ units ($\Delta AIC_c$) of the best model (i.e., the model with the lowest $AIC_c$—Burnham and Anderson 1998). We also calculated the AIC weight ($w_i$), which provides a measure of the strength of evidence for a model.

We used program PRESENCE 2.3 (Hines 2006) to model occupancy and account for imperfect detection. We estimated the proportion of sites occupied ($\Psi$) and probability of detection ($p$) for marsh rice rats at 43 sites using methods developed by MacKenzie et al. (2002). We included only 43 of 48 sites in the occupancy modeling analysis because flooding prevented collection of microhabitat data at 5 sites near Mermet Lake, Massac County, Illinois.

Each day of the 5-day trapping session was considered a part of a repeated survey. We then constructed encounter histories based on overall detection or nondetection. If at least 1 rice rat was captured in a given day, the survey was assigned a 1, meaning rice rats were detected. If no rice rats were captured, the survey was assigned a 0, meaning rice rats were not detected. When sessions lasted longer than 5 days, only the first 5-day interval was used to create the encounter history. At sites where multiple trapping sessions occurred, the trapping session that included the 1st rice rat encounter was used for the detection history (Winchester et al. 2009).

We used 3 sampling covariates—date, breeding season, and possibility of recapture—to model parameter $p$. Sampling covariates can change from one survey to the next, even at the same site. Breeding season was considered May–October. A possibility of recapture during a survey existed if a rice rat had been captured at that site in any previous survey. To examine the impact of these covariates on $p$ we held occupancy constant ($\Psi[.]$) and ran a candidate set of 4 models. In 1 of these models $p$ was constant ($p[.]$). In the remaining 3 models, $p$ was a function of the sampling covariates.

The most-parsimonious site covariate model of $p$ was retained to use in modeling $\Psi$ as a function of the habitat covariates. We constructed a candidate set of 13 models based on results of the logistic regression analysis and possible biological importance to rice rats. In one model, occupancy was held constant ($\Psi[.]$). In the remaining 12 models, $\Psi$ was a function of $\geq 1$ habitat covariates (% bare ground, % herbaceous cover, % visual obstruction at 0.0–0.5 m, AG, DEV, PEME, UP_GRASS, WATER; Table 1). All data were transformed for normality using the arcsine square-root transformation. We tested the global model from the candidate set of models using the MacKenzie and Bailey (2004) goodness-of-fit test in PRESENCE 2.3.

## RESULTS

*Capture and density estimation.*—We captured 132 (56 females and 76 males) individual rice rats 192 times in 13,248 trap nights. Capture success was 14.49 captures/1,000 trap nights. Body mass for females averaged ($\pm SE$) 54.1 $\pm$ 1.9 g ($n = 10$) for reproductive and 44.8 $\pm$ 1.7 g ($n = 44$) for nonreproductive females (2 females were not classified by reproductive status). Body mass for males averaged 56.4 $\pm$ 2.2 g ($n = 25$) for reproductive and 50.6 $\pm$ 1.6 g ($n = 51$) for nonreproductive males. The minimal body mass for reproductive males and females was 38 and 47 g, respectively.

We detected rice rats at 16 (5 random and 11 historical) of 48 sites (33.3%; Fig. 1). We captured rice rats at 6 (28.6%) of 21 sites in the Big Muddy watershed, 3 (100%) of 3 sites in the Cache watershed, 2 (15.4%) of 13 sites in the Mississippi watershed, 1 (16.7%) of 6 sites in the Ohio watershed, and 4 (80.0%) of 5 sites in the Saline watershed (Fig. 1). Rice rats were captured in 23 separate transects in the 16 occupied sites. These transects were located in palustrine emergent (PEM; $n = 12$), palustrine unconsolidated bottom–intermittently exposed (PUBG; $n = 9$), palustrine forested (PFO; $n = 1$), and riverine unconsolidated bottom (R2UB; $n = 1$) wetlands. Relative abundance ranged from 1.74 to 91.41 individuals/ 1,000 trap nights. Minimum density estimates ranged from 0.13 individual/ha (a single individual) to 1.74 individuals/ha (22 individuals).

We trapped within 15 mine-associated wetland complexes throughout this study. Nine (60.0%) of these 15 sites were occupied by marsh rice rats, whereas rice rats were captured at 7 (20.0%) of 33 sites in wetland complexes not associated with coal-mining practices. The presence of rice rats was

TABLE 2.—Logistic regression results for microhabitat measurements influencing occurrence of marsh rice rats (*Oryzomys palustris*) in southern Illinois, 2007–2009. Models are sorted from lowest to highest Akaike information criterion (AIC$_c$) value. $K$ represents number of parameters in the model, and $w_i$ represents the Akaike weighting factor of the model.

| Model | $K$ | $R^2$ | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ |
|---|---|---|---|---|---|
| % visual obstruction 0–0.5 m | 2 | 0.11 | 56.27 | 0.00 | 0.23 |
| % herbaceous cover | 2 | 0.09 | 57.19 | 0.92 | 0.15 |
| % herbaceous cover + % visual obstruction 0–0.5 m | 3 | 0.12 | 57.70 | 1.43 | 0.12 |
| % bare ground + % rock | 3 | 0.12 | 58.03 | 1.77 | 0.10 |
| % bare ground | 2 | 0.07 | 58.10 | 1.84 | 0.09 |
| % visual obstruction 0–0.5 m + % visual obstruction 0.5–1.0 m + % visual obstruction 1.0–1.5 m | 4 | 0.15 | 58.97 | 2.70 | 0.06 |
| % rock | 2 | 0.04 | 59.32 | 3.05 | 0.05 |
| Distance to water + % herbaceous cover | 3 | 0.09 | 59.54 | 3.27 | 0.05 |
| % visual obstruction 0.5–1.0 m | 2 | 0.01 | 60.54 | 4.28 | 0.03 |
| % leaf litter | 2 | 0.01 | 60.56 | 4.29 | 0.03 |
| % shrub | 2 | 0.01 | 60.71 | 4.44 | 0.03 |
| Stems per hectare | 2 | 0.002 | 61.00 | 4.74 | 0.02 |
| % visual obstruction 1.0–1.5 m | 2 | 0.002 | 61.01 | 4.75 | 0.02 |
| Distance to water | 2 | 0.0003 | 61.06 | 6.36 | 0.02 |

associated strongly with mining practices ($\chi^2_1 = 6.98$, $P = 0.008$) and the presence of common reed within 50 m of the trapping grid ($\chi^2_1 = 7.61$, $P < 0.01$). Only 2 key wetland species, common reed and sedges, occurred at higher rates at occupied sites. Common reed occurred in 31.4% of quadrats at occupied sites versus 12.1% of quadrats at unoccupied sites, whereas sedges occurred in 22.6% of quadrats at occupied sites versus 8.5% of unoccupied sites.

*Habitat associations and occupancy.*—Ten single-parameter models and 4 multiple-parameter models comprised the microhabitat variable candidate set. Of these models, the model with the lowest AIC$_c$ value contained % visual obstruction at 0.0–0.5 m as the independent variable. However, we detected only moderate to weak support for this variable affecting rice rat occurrence ($w_i = 0.23$). Four other models were within 2 $\Delta$AIC$_c$ of the lowest model (Table 2). The 2 variables that composed the top 3 models had positive model coefficients (% visual obstruction $\beta = 0.04$, % herbaceous cover $\beta = 0.04$) and had higher (% visual obstruction: $t_{36.3} = 2.56$, $P = 0.01$; % herbaceous cover: $t_{40.2} = 2.18$, $P = 0.01$) average levels on occupied sites.

The landcover variable candidate set consisted of 18 models (Table 3). The model with the lowest AIC$_c$ value (59.00) was a single-variable model composed of total area of upland grass within the 50-ha circular buffer (UP_GRASS; Table 3). All models within 2 $\Delta$AIC$_c$ (0.92–1.59) of the top model (AG + DEV + UP_GRASS, NON_FOR + UP_GRASS, PEMA + PEME + PSS + UP_GRASS, PEMA + PEME + UP_GRASS) contained the UP_GRASS parameter. The mean area of upland grass within the 50-ha buffer was 9.68 ± 2.90 ha ($n = 16$) at occupied sites but only 2.92 ± 1.10 ha ($n = 32$) at unoccupied sites ($t_{19.4} = 2.18$, $P = 0.04$). All landcover variables in the top models had positive coefficients relative to rice rat occurrence except for agricultural area in the buffered zone. The top-ranked AIC$_c$ model had moderate to weak support of affecting rice rat occurrence ($w_i = 0.26$), and all other models within 2 $\Delta$AIC$_c$ had weak support of affecting rice rat occurrence ($w_i$ range = 0.06–0.13; Table 3).

Two models with detection probability as a function of sampling covariates were stronger than the model with $p$ constant. The strongest model from the detection probability candidate set was ($\Psi$[.], $p$[Recap]). Therefore, the sampling covariate ($p$[Recap]) was used in all occupancy models with $\Psi$ as a function of habitat covariates. Detection probability was lowest on day 1 (0.44 ± 0.12) and highest on day 4 (0.87 ± 0.08) of the 5-day trapping sessions. Habitat covariates had an influence on occupancy, and 8 models that included habitat covariates were stronger than the model that held $\Psi$ constant (Table 4). The best overall model for predicting rice rat occupancy was ($\Psi$[%Herb + UP_GRASS], $p$[Recap]), which was consistent with the results of the logistic regression

TABLE 3.—Logistic regression results for landcover types influencing occurrence of marsh rice rats (*Oryzomys palustris*) in southern Illinois, 2007–2009. Landcover types were recorded within a 50-ha circular buffer from the center of the trapping grid. Models sorted from lowest to highest Akaike information criterion (AIC$_c$) value. $K$ represents number of parameters in the model, and $w_i$ represents the Akaike weighting factor of the model.

| Model | $K$ | $R^2$ | AIC$_c$ | $\Delta$AIC$_c$ | $w_i$ |
|---|---|---|---|---|---|
| UP_GRASS | 2 | 0.12 | 59.00 | 0.00 | 0.26 |
| AG + DEV + UP_GRASS | 4 | 0.17 | 59.92 | 0.92 | 0.13 |
| NON_FOR + UP_GRASS | 3 | 0.14 | 60.11 | 1.11 | 0.11 |
| PEMA + PEME + PSS + UP_GRASS | 5 | 0.20 | 60.49 | 1.49 | 0.06 |
| PEMA + PEME + UP_GRASS | 4 | 0.16 | 60.59 | 1.59 | 0.06 |
| AG | 2 | 0.07 | 61.89 | 2.89 | 0.06 |
| PFO | 2 | 0.06 | 62.11 | 3.11 | 0.05 |
| DEV | 2 | 0.05 | 62.51 | 3.51 | 0.04 |
| PEME | 2 | 0.04 | 62.99 | 3.99 | 0.03 |
| WATER | 2 | 0.04 | 63.18 | 4.18 | 0.03 |
| PEME + WATER | 3 | 0.08 | 63.30 | 4.40 | 0.03 |
| PEMA | 2 | 0.03 | 63.71 | 4.71 | 0.02 |
| PEMA + PEME | 3 | 0.06 | 63.89 | 4.89 | 0.02 |
| TOT_WET | 2 | 0.02 | 63.98 | 4.98 | 0.02 |
| PFO + UP_FOR | 3 | 0.06 | 64.01 | 5.01 | 0.02 |
| PSS | 2 | 0.01 | 64.46 | 5.46 | 0.02 |
| NON_FOR | 2 | 0.01 | 64.59 | 5.59 | 0.02 |
| UP_FOR | 2 | <0.01 | 65.05 | 6.05 | 0.01 |

TABLE 4.—Model selection results for competing models of habitat covariates influencing occupancy ($\Psi$) while maintaining the most-parsimonious site covariate detection model for marsh rice rats (*Oryzomys palustris*) captured during 2007–2009 survey in southern Illinois. Models sorted from lowest to highest Akaike information criterion ($AIC_c$) value. $K$ represents number of parameters in the model, and $w_i$ represents the Akaike weighting factor of the model.

| Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| $\Psi$(%Herb + UP_GRASS) $p$(Recap) | 5 | 125.92 | 0.00 | 0.7048 |
| $\Psi$(%0.5mVO) $p$(Recap) | 4 | 128.21 | 2.29 | 0.2243 |
| $\Psi$(UP_GRASS) $p$(Recap) | 4 | 131.92 | 6.00 | 0.0351 |
| $\Psi$(Global) $p$(Recap) | 11 | 133.11 | 7.19 | 0.0194 |
| $\Psi$(AG) $p$(Recap) | 4 | 135.50 | 9.58 | 0.0059 |
| $\Psi$(% Bare) $p$(Recap) | 4 | 136.09 | 10.17 | 0.0044 |
| $\Psi$(% Herb) $p$(Recap) | 4 | 136.58 | 10.66 | 0.0034 |
| $\Psi$(DEV) $p$(Recap) | 4 | 138.15 | 12.23 | 0.0016 |
| $\Psi$(.) $p$(Recap) | 3 | 140.13 | 14.21 | 0.0006 |
| $\Psi$(WATER) $p$(Recap) | 4 | 141.17 | 15.25 | 0.0003 |
| $\Psi$(PEME) $p$(Recap) | 4 | 142.05 | 16.13 | 0.0002 |
| $\Psi$(PEME + WATER) $p$(Recap) | 5 | 142.99 | 17.07 | 0.0001 |
| $\Psi$(AG + DEV + UP_GRASS) $p$(Recap) | 6 | 154.45 | 28.53 | 0.0000 |

analyses. This model estimated $\Psi$ to be 0.374, which compares with the naïve estimate of 0.372 (rice rats captured at 16 of 43 sites for which we collected microhabitat measurements).

The influence of individual habitat covariates on occupancy was determined by summing $AIC_c$ model weights. The individual habitat covariates that had the most influence on occupancy were UP_GRASS (w + [i] = 0.74) and % herbaceous cover (w + [i] = 0.73), which were also the most influential variables in the logistic regression analysis. Both variables positively influenced rice rat occupancy.

## DISCUSSION

Our site-selection process incorporated previous ecological knowledge about rice rats and was designed to determine which types and features of local wetlands were associated with rice rat occurrence. Therefore, it included random wetland-dominated sites that were not optimal habitat. Also, optimal habitat can change temporally due to yearly or seasonal changes in vegetation structure. In comparison, Hofmann et al. (1990) trapped opportunistically in areas where rice rat occupancy was probable based on direct field observation. These sites, if unmanaged, had undergone >20 years of succession by the time we trapped at these locations. For example, sites once dominated by grasses, sedges, and rushes (Hofmann et al. 1990) often had undergone succession to shrub-dominated communities including species such as black willow (*Salix nigra*), red maple (*Acer rubrum*), buttonbush, and sycamore (*Platanus occidentalis*). This change in vegetation composition could have led to local extirpation of rice rats, because the species rarely was found in wetlands dominated by woody species.

The site-selection process and successional changes in habitat on historical sites could have contributed to lower capture rates and rice rat occupancy in this study than in the last extensive survey of southern Illinois (Hofmann et al. 1990). Hofmann et al. (1990) captured 28.2 rice rats/1,000 trap nights at 13 of 31 (naïve occupancy = 0.419) sites. Broader comparisons showed that the capture rate (10.0 individual rice rats/1,000 trap nights) during our entire study (2007–2009) was lower than capture rates reported in coastal areas across the range, which varied from 21.7 rice rats/1,000 trap nights (Kruchek 2004) to 68.4 rice rats/1,000 trap nights (Bloch and Rose 2005; Table 5). Capture rates in early-successional habitats in a bottomland hardwood forest in the Mississippi River Delta region were 67 rice rats/1,000 trap nights (total effort = 539 trap nights) prior to a flood event (Chamberlain and Leopold 2003). Similarly, density estimates in the present study, which represent minimum estimates, were much lower than densities reported from other studies (Table 5). Our occupancy modeling indicated that because daily detection probabilities

TABLE 5.—Marsh rice rat (*Oryzomys palustris*) capture rates and densities from previous published studies and the present study.

| Location | Habitat type | Individuals/1,000 trap nights | Density (*n*/ha) | Reference |
|---|---|---|---|---|
| Coastal | | | | |
| Louisiana | Coastal marsh | 53.0 | | Martin et al. (1991) |
| Louisiana | Sedge community | | 17.8 | Negus et al. (1961) |
| Maryland | Coastal marsh | 11.5–49.2 | | Harris (1953) |
| Mississippi | Tidal marsh | 62.0 | 2, 25[a] | Wolfe (1985) |
| Texas | Coastal wetland | 21.7 | 10.5 | Kruchek (2004) |
| | Adjacent upland | | 3.1 | |
| Texas | Coastal prairie (inundated) | | 28.8 | Abuzeineh et al. (2007) |
| | Coastal prairie (water receded) | | 49.2 | |
| Virginia | Tidal marsh (Townsend) | 68.4 | 8, 87[a] | Bloch and Rose (2005) |
| | Tidal marsh (Oyster) | 20.7 | 3, 15[a] | Bloch and Rose (2005) |
| Inland | | | | |
| Arkansas | Pine plantation | 0.02 | | Miller et al. (2004) |
| Florida | Hardwood hammocks | 12–57 | | Smith and Vrieze (1979) |
| Georgia | Pine plantation | 0.27 | | Atkenson and Johnson (1979) |
| Illinois | Palustrine wetlands | 10.0 | | Present study |
| Mississippi | Early successional hardwood forest | 67.0 | | Chamberlain and Leopold (2003) |

[a] Numbers represent spring and fall densities, respectively.

(*p* range = 0.44–0.87) were high, rice rats most likely would be detected if they occurred within a sampling site. Studies of overwinter survival, density, and habitat use are needed to better understand differences that might exist between core and peripheral populations within the species' range.

Previous research has documented strong positive associations between rice rats and dense herbaceous cover near wetlands (Hofmann et al. 1990; Negus et al. 1961; Svihla 1931). Our work confirmed these associations in freshwater wetlands in Illinois and added to our knowledge of the ecology of marsh rice rats by examining links between microhabitat and landcover variables relative to rice rat occupancy. Although our models were relatively weak, the strongest positive predictors of rice rat occurrence at the microhabitat level were % visual obstruction from 0.0–0.5 m and % herbaceous cover. Svihla (1931) reported that rice rats in southern Louisiana were located in dense vegetation that provided food and cover. Hofmann et al. (1990) reported that many occupied sites were dominated by emergent vegetation such as sedges, rushes, cattails, and common reed.

Knowing that the marsh rice rat is a wetland-obligate species, we also focused on determining which wetland or other landcover types in the surrounding landscape were most associated with rice rat occurrence. Although nearly all captures of rice rats were made in early successional wetlands, no models based solely on wetland-type parameters were among the top candidates in the landcover candidate set. This apparent anomaly likely was due to our a priori site-selection process, which included the use of historic sites that were in or near wetlands and a criterion of 20 ha of wetlands within a 50-ha buffer around random points. The importance of upland grass cover in the landscape surrounding the trapping sites was not surprising given that we sampled sites dominated by the preferred wetland vegetation of rice rats. Uplands can be used as refugia during periods of high water and as sink habitats for dispersers (Kruchek 2004), or used by transients (Wolfe 1982). Rice rats also feed in uplands on vegetation such as eastern gamagrass (*Tripsacum dactyloides*) and wild-rye (*Elymus virginicus*), or on insects and berries (Hamilton 1946; Kincaid and Cameron 1982). They forage in uplands when using them as refugia or during reproductive periods when nutrient demands are highest (Kruchek 2004).

Other landcover models were given less support but provided some insight into habitat selection by rice rats. Other competing models were consistent with previous work demonstrating that early successional wetlands (e.g., palustrine emergent types) are important for marsh rice rats (Hofmann et al. 1990; Svihla 1931), with the presence of emergent plants such as common reed and sedges being highly associated with rice rat occurrence. The positive relationship of developed areas with occurrence likely was due to roads being classified as developed. Rice rats were captured within roadside ditches in our study and by Hofmann et al. (1990). Roadside ditches that occur within larger wetland complexes often contain vegetation and hydrologic conditions suitable for rice rats. For example, emergent vegetation in ditches where

rice rats were captured included sedges, rushes, bulrushes (*Scirpus* spp.), spike rushes (*Eleocharis* spp.), and cattails (Hofmann et al. 1990). Therefore, developed areas are not necessarily good habitat, but roadside ditches might provide sufficient cover.

*Conservation implications.*—This study provides relevant data regarding rice rat conservation in inland, freshwater regions of the species' range within the United States. We propose that metapopulations (Hanski 1999) of rice rats are spatially clustered throughout the inland southeastern United States in appropriate wetland complexes. The range map for the marsh rice rat in Hall (1981) displays a contiguous range throughout the southeastern United States. However, it is extremely unlikely that this species occurs throughout this entire area, especially in the foothills of the Appalachian Mountains in northern Georgia and southwestern Tennessee. The species has been recognized for decades as an effective disperser and colonizer in coastal (Loxterman et al. 1998; Negus et al. 1961) and inland (Smith and Vrieze 1979) island systems, leading Kruchek (2004) to discuss persistence of rice rats in terms of metapopulation biology. Local populations might be at some risk of extinction (Kruchek 2004). However, the overall population could persist because risk of extinction is spread throughout many different populations, providing overall stability for the species (Hanski 1999). Improving connectivity between wetland complexes could benefit rice rats by facilitating expansion of metapopulations to currently unoccupied but suitable habitat. In addition, understanding dispersal of rice rats and their response to hydrologic regimes would enable conservation scientists to focus resources on areas that would benefit existing rice rat populations.

Rice rats undoubtedly benefit from the construction, restoration, and protection of emergent wetlands, often under the umbrella of management practices directed toward more economically valuable species, such as waterfowl, that prefer wetland habitats. These practices include the federal Wetland Reserve Program, wetland mitigation, and wetland restoration associated with mined lands. For example, we recorded rice rats in actively managed moist-soil wetlands designed to provide habitat for migrating shorebirds and waterfowl. Historical wetland loss has negatively affected rice rat populations in Illinois and other parts of its range. However, since the listing of the species as state-threatened in Illinois in 1978, wetland area in southern Illinois has increased because of the Wetland Reserve Program, which is designed to create, enhance, or restore wetlands. From 1992 to 2007 the Natural Resources Conservation Service spent more than $10,000,000 on 270 contracts to enroll 25,286 ha in Illinois into this program (Natural Resources Conservation Service 2009). This increase in wetlands might have benefited rice rat populations enough that they are no longer at risk for extirpation in Illinois.

Restoration and development of wetlands associated with surface coal-mine reclamation since the 1970s likely benefited populations of marsh rice rats in inland regions of the species' range by creating long-term rice rat habitat. Many coal-mining practices, such as subsidence, surface-mine sediment ponds,

and slurry ponds provide seasonal and permanent wetlands (Nawrot and Klimstra 1989) that are often surrounded by emergent vegetation such as common reed. We noted a strong positive link among rice rat occurrence, reclaimed mines, and emergent vegetation. Many reclaimed mine locations have more wetland area than before the initiation of active mining, and it is likely that rice rats recently (within the last 30 years) have colonized these areas (Urbanek and Klimstra 1986).

Rice rats also can benefit from grassland restoration practices near wetlands. Our finding that upland grasslands adjacent to wetland areas are important to rice rats support related findings in a coastal system (Kruchek 2004). They also confirm previous recommendations to incorporate upland buffers into wetland delineations for enhanced protection of reptiles (Burke and Gibbons 1995), amphibians (Semlitsch 1998), and mammals (Kruchek 2004) that use the wetland–upland interface.

## ACKNOWLEDGMENTS

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