

## Golden mice (*Ochrotomys nuttalli*) co-occurrence with *Peromyscus* and the abundant-center hypothesis

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Golden mice (*Ochrotomys nuttalli*) occur throughout the southeastern United States, and are on the periphery of their geographic range in southern Illinois, where they are a state-listed threatened species. We assessed relative abundance and distribution of populations of golden mice in southern Illinois by mark–recapture and occupancy models, and throughout the core geographic distribution to determine if they should be removed from threatened status (delisted). We also tested the “abundant-center” hypothesis that states that occurrence and abundance of a species is greater in the core of the range than at the periphery. We captured golden mice in 21 of 24 sites in southern Illinois, but only 13 of 24 sites in the core of the range. The total number of individual golden mice captured in southern Illinois ( $n = 99$ ) was 3.3 times greater ( $\chi^2_1 = 36.91$ ,  $P < 0.001$ ) than in the core ( $n = 30$ ). Habitat factors at sites (mean number of climbing vines, woody stems, and herbaceous stems) affected occupancy of golden mice; no model variables affected occupancy of sympatric *Peromyscus*. Based on occupancy models, the probability of capturing golden mice was not affected by occurrence of the potential interspecific competitors white-footed mice (*Peromyscus leucopus*) or cotton mice (*P. gossypinus*). Our results for occurrence and abundance of golden mice at the periphery of their range in Illinois do not support the abundant-center hypothesis.

Key words: abundant-center hypothesis, occupancy models, *Ochrotomys nuttalli*, *Peromyscus gossypinus*, *Peromyscus leucopus*

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Golden mice (*Ochrotomys nuttalli*) are generally considered to be rare throughout their range. Definitions of “rarity” vary (Gaston 1994); nonetheless, species of conservation concern such as the golden mouse may actually have low abundance, appear to be rare because of local or range-wide spatial clustering, or exhibit temporal variation in abundance (Feldhamer and Morzillo 2008). As noted by Rabinowitz et al. (1986), a species falls on the continuum from abundant to rare depending on the extent of its geographic distribution, local population abundance, and range of habitats occupied. As such, mammalian species with a narrow geographic range, low abundance, and few occupied habitats will be rare (Yu and Dobson 2000). Regardless of whether a species is considered abundant or rare, however, levels of abundance and occurrence often are considered to be highest in the center of the geographic range and decline toward the periphery (Brown 1984; Gaston 1994; Guo et al. 2005; Hengeveld and Haeck 1981). Although defining the center of a species’ range can be

problematic (Sagarin et al. 2006), this “abundant-center hypothesis” is often embraced as a “rule of thumb,” a “biological rule,” or a characteristic “shared by all species” (see Sagarin and Gaines 2002, 2006).

Golden mice have a relatively large geographic range for a small, temperate zone rodent. They are distributed throughout the southeastern United States from eastern Texas and Oklahoma along the Gulf Coast to central Florida and north to central Virginia and Kentucky (Feldhamer and Linzey 2008). The species is listed as state-threatened in Illinois (Herkert 1992) based on limited distribution in the state, perceived low population density, unique habitat requirements, and because it is at the northernmost edge of its range in the midwestern United States.



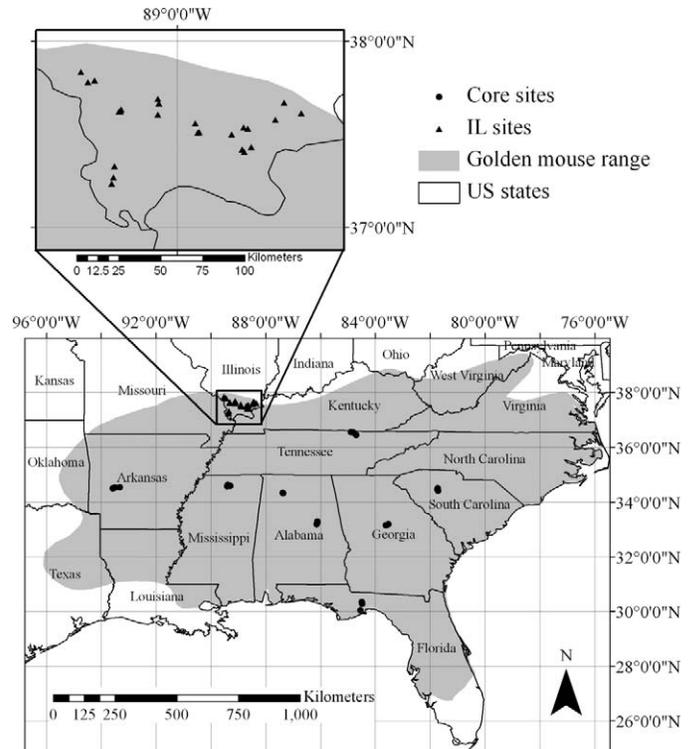
Past studies in Illinois and the core of the range indicate that local populations of golden mice vary in abundance and other population parameters spatially and temporally (Feldhamer and Linzey 2008). Although it may vary considerably, abundance of golden mice is generally low relative to that of white-footed mice (*Peromyscus leucopus*) or other sympatric *Peromyscus* spp. (Rose 2008), and this difference is often attributed to interspecific competition (Christopher and Cameron 2008).

Locally occupied habitats of golden mice vary widely, and the tendency to be considered a habitat generalist or specialist again seems to be highly site specific. Generally, however, golden mice have been considered to be habitat specialists (Dueser and Hallett 1980; Knuth and Barrett 1984; Seagle 1985), selecting dense understory and vines in deciduous hardwood and coniferous forests. Thick understory is considered a necessary component of golden mouse habitat (Linzey and Packard 1977; McCarley 1958), with the vertical structure providing access between arboreal nests and ground cover, a food supply, and possible protection from predators (Morzillo et al. 2003; Wagner et al. 2000).

We assessed relative abundance and distribution of populations in Illinois—on the periphery of their geographic distribution—in comparison with populations throughout their core geographic range. Our objectives were to determine if golden mice should be delisted in Illinois based on the percentage of sampled sites they occupied and their relative abundance; the habitat factors affecting occurrence; and the influence of sympatric *Peromyscus* spp. on occupancy of golden mice. Our data on golden mice also provided an opportunity to test the abundant-center hypothesis. Few previous studies of mammals have examined this concept with sites sampled from throughout much of a species' range (Gaston 1994; Sagarin and Gaines 2002).

## MATERIALS AND METHODS

**Study sites.**—We used geographic information system data layers and the United States Geological Survey's Gap Analysis Program (<http://gapanalysis.usgs.gov>) to determine appropriate forested habitats with dense understory cover as potential trapping sites for golden mice in Illinois and throughout their core area in the southeastern United States (Fig. 1). We selected 24 sites in Illinois (Appendix I), and 24 sites throughout the core area in Arkansas, Alabama, Florida, Georgia, Mississippi, South Carolina, and Tennessee (Appendix II). All sites in Illinois were selected on public land (Shawnee National Forest, Crab Orchard National Wildlife Refuge, and Cypress Creek National Wildlife Refuge) and within 0.4 km of a road for accessibility. We chose Illinois sites without regard to previous studies where golden mice had been collected. Similar criteria were used to select the sites in the core of the geographic range. Also, with the exception of the 3 sites in Liberty County, Florida, core sites were  $\geq 100$  km inland from the "edge" of the geographic range of golden mice so they would not be peripheral populations.



**FIG. 1.**—Site locations for livetrapping golden mice (*Ochrotomys nuttalli*) and *Peromyscus* in southern Illinois (inset) from April through October 2008 and throughout the southeastern United States from May through October 2009. See Appendixes I and II for county locations and Universal Transverse Mercator (UTM) coordinates.

**Livetrapping procedures.**—Trapping in Illinois was conducted during April–October 2008. Grids were  $60 \times 60$  m with 10 m between trap stations for a total of 49 traps per grid. During each session, live traps were set for 5 consecutive nights on each grid; we considered each grid as a site in modeling procedures. After we sampled all 24 sites once, the process was repeated so that we trapped on each site a total of 10 days. We placed 1 large ( $8 \times 9 \times 23$ -cm) Sherman live trap (H. B. Sherman Traps Inc., Tallahassee, Florida) at each trap station. Traps were placed within 2 m of exact station locations and were elevated in trees or vine masses to increase the likelihood of capturing golden mice when possible. Traps were baited with a mixture of sunflower seeds and cracked corn and contained polyfiber batting to aid in thermoregulation. Captured animals were marked with a Monel ear tag (model 1005-1; National Tag and Band, Newport, Kentucky) and their species, sex, weight, reproductive condition, and trap location were recorded. Marked individuals were released at the point of capture. The protocol for trapping and handling small mammals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Institutional Animal Care and Use Committee of Southern Illinois University Carbondale (protocol 07-045). Appropriate trapping permits were obtained from all states.

We sampled sites throughout the core of the range during May–October 2009, with the same trapping protocol as in

Illinois. As in Illinois, we trapped on all core sites for 10 days for a total of 23,520 trap nights for the study. During the 2nd trapping survey on all sites, we measured habitat variables that may have influenced site occupancy of golden mice and *Peromyscus* spp. We recorded habitat variables at 10 randomly selected trap stations on each site. We based vegetation variables on those commonly associated with golden mice (Dueser and Hallett 1980; Wagner et al. 2000). We measured rooted herbaceous (HSTEM) and woody stem counts (WSTEM) within a 3-m-radius circular plot centered at each of the randomly selected trap stations. We visually estimated percent canopy cover (CANOPY) directly above trap stations. We visually estimated the number of rooted or unrooted climbing vines (VINE) within a 1-m radius of each trap station. An average value for each variable was then calculated for each site. We also measured diameter at breast height (DBH) of the nearest tree to each trap.

**Data analyses.**—Few sites had adequate numbers of golden mice, white-footed mice, or cotton mice (*Peromyscus gossypinus*) to allow for mark–recapture density estimates. Instead, we considered relative abundance on a site as the number of individuals of each species captured because trapping effort was equal across sites and areas. Because detection of most species is imperfect and likely varies among species and sites based on abundance (Royle and Nichols 2003), we used occupancy modeling (MacKenzie et al. 2002, 2006) to estimate the proportion of sites occupied and the probability that a site was occupied ( $\psi$ ) by golden mice and sympatric *Peromyscus* spp. assuming that each species had a detection probability ( $p$ ) < 1 when present. We grouped white-footed mice and cotton mice as “ecological equivalents” based on similar phylogeny (Carleton 1989; Zimmerman et al. 1978) and behavior (Layne 1969; Layne and Ehrhart 1970; Lovecky et al. 1979; Wolfe 1970), and because they hybridize in the wild (Barko and Feldhamer 2002; Dice 1940). Additionally, grouping avoided the possibility of misidentification (Fernandes et al. 2010) of these species in the field.

As noted, all 48 sites were visited 10 times (two 5-day trapping periods); if at least 1 individual of a species was trapped on 1 of the 10 days, we considered the site occupied. As suggested by MacKenzie et al. (2006), we used robust-design models to verify that occupancy was closed between trapping surveys. We standardized all continuous covariates to z-scores before analysis, thereby interpreting model coefficients as the change in the log-odds ratio of occupancy relative to 1 standard deviation change in the covariate from its mean (Cooch and White 2005).

In a 3-stage modeling procedure, we used an information-theoretic approach to develop a priori models for  $p$  and  $\psi$  with combinations of livetrapping variables—including region (REG: Illinois or the core of the range), species previously detected at the site  $\geq 1$  time (PDET), Julian date (DATE), and whether trapping was the 1st or 2nd round (SURVEY)—and habitat factors that may affect  $\psi$  and  $p$  for golden mice and *Peromyscus*, and factors that may influence species co-occurrence. We used program PRESENCE 3.1 (Hines 2006)

to rank models in each stage based on their Akaike’s information criterion adjusted for small sample size (AIC<sub>c</sub>) values, and model weights ( $w_i$ s) to select the most-supported model and calculate model-averaged  $p$  and  $\psi$  estimates (Burnham and Anderson 2002; MacKenzie et al. 2006). The  $w_i$  for each model represented the probability of that model being the best of those evaluated. First, we held occupancy constant ( $\psi(\cdot)$ ) and used detection histories and survey-specific data to develop species-specific probabilistic models of  $p$ . We fit  $p$  models with combinations of PDET, REG, DATE, and SURVEY data. We used the most-supported species-specific  $p$  model for subsequent stages.

Second, we fit species-specific detection histories to a priori candidate model sets that included various combinations of region and vegetation characteristics that may affect  $\psi$ . Finally, we used presence of *Peromyscus* spp. as an explanatory variable in species co-occurrence models to estimate their influence on the occupancy dynamics of golden mice. Because imperfect detection of target species could lead to misleading inferences about species co-occurrence patterns, we accounted for species-specific detection probabilities while modeling multispecies site occupancy (MacKenzie et al. 2004, 2006). We estimated the level of species co-occurrence by:

$$\phi = \psi^{AB} / \psi^A \times \psi^B,$$

where  $\psi^A$  and  $\psi^B$  are probabilities of site occupancy by species A and B, respectively, and  $\psi^{AB}$  is the probability that a site is occupied by both species. If species co-occur randomly,  $\phi = 1$ . Using AIC<sub>c</sub> values and model weights, we compared the most-supported co-occurrence plus habitat models with the most-supported habitat-only occupancy models for golden mice and *Peromyscus* spp. to determine the relative importance of habitat versus species interactions.

We compared captures in elevated versus ground-placed traps, and compared total captures and number of occupied sites for each species in Illinois versus the core of the range using chi-square tests. We used a  $t$ -test to determine differences in persistence of golden mice on sites between the 1st and 2nd surveys in Illinois and the core of the range, and to compare mean high temperatures of sites during the 1st and 2nd surveys. We used daily temperature data from the National Oceanic and Atmospheric Administration’s National Climatic Data Center (<http://www.noaa.gov>) from the weather station nearest to each site.

## RESULTS

We caught 99 golden mice 190 times ( $n = 91$  recaptures) on the 24 sites in Illinois (Table 1). Of these captures, 174 (91.6%) were in elevated traps rather than traps placed on the ground ( $\chi^2_1 = 23.53$ ,  $P < 0.001$ ). We captured  $\geq 1$  golden mouse on 21 (87.5%) of the 24 sites in Illinois, with 1–15 individuals per site (Appendix I). We also caught *P. leucopus* ( $n = 244$ ; Table 1) on all 24 Illinois sites, with 3–21 individuals per site.

On the 24 sites in the core of the range, we caught only 30 individual golden mice (Table 1), fewer than in Illinois ( $\chi^2_1 =$

**TABLE 1.**—Total captures of golden mice (*Ochrotomys nuttalli*), white-footed mice (*Peromyscus leucopus*), and cotton mice (*P. gossypinus*) on all sites in Illinois ( $n = 24$ ) during 2008 and the core of the range ( $n = 24$ ) during 2009. Ancillary species captured are not listed. Total number of trap nights was 11,760 in each region.

Region	Species	No. individuals	Total captures (marked + recaptures)
Illinois (2008)	<i>Ochrotomys nuttalli</i>	99	190
	<i>Peromyscus leucopus</i>	244	547
Core range (2009)	<i>Ochrotomys nuttalli</i>	30	62
	<i>Peromyscus leucopus</i>	44	142
	<i>Peromyscus gossypinus</i>	21	38

36.91,  $P < 0.001$ ). Thirteen (54.2%) of the 24 sites throughout the core had  $\geq 1$  golden mouse; numbers of individuals ranged from 1 to 6 (Appendix II). We found no difference in the number of occupied sites in Illinois versus the core of the range ( $\chi^2_1 = 1.88$ ,  $P = 0.17$ ). In Illinois, 44 (57.1%) of the 77 golden mice taken during the initial round of trapping persisted on the sites and were recaptured during the 2nd round (Appendix I) compared to only 7 (33.3%) of 21 in the core of the range, a significant difference ( $t_{1,46} = 3.36$ ,  $P < 0.002$ ). We also caught fewer *Peromyscus* spp. ( $n = 65$ ; Table 1) throughout the core ( $\chi^2_1 = 65.67$ ,  $P < 0.001$ ). There was no difference in mean high temperatures between Illinois and core sites for months that encompassed either the 1st survey ( $t_{1,70} = 0.698$ ,  $P = 0.487$ ) or the 2nd ( $t_{1,70} = 0.981$ ,  $P = 0.329$ ).

Detection probabilities of golden mice and *Peromyscus* spp. were influenced by the same factors in similar ways, including region, previous detection, date, and survey (Table 2). Model selection including only white-footed mice or only cotton mice was not significantly different from models for these 2 species combined. We discuss only the combined models (full model selection results are available from the authors). Consistent with the naïve trapping results, detection was higher in Illinois than in the core (golden mice, Illinois  $p = 0.457 \pm 0.035$ , core  $p = 0.331 \pm 0.049$ ; *Peromyscus* spp., Illinois  $p = 0.713 \pm 0.030$ , core  $p = 0.441 \pm 0.035$ ). Detection probability also was

higher early in the field season than late (golden mice, early  $p = 0.504 \pm 0.040$ , late  $p = 0.330 \pm 0.037$ ; *Peromyscus* spp., early  $p = 0.641 \pm 0.033$ , late  $p = 0.527 \pm 0.034$ ).

Model-averaged occupancy estimates for golden mice ( $\psi = 0.808 \pm 0.085$ ) and *Peromyscus* spp. ( $\psi = 0.824 \pm 0.017$ ) were similar. Although most habitat models received more support than the null model, there was no dominant golden mouse occupancy model. Several models had similar support, suggesting that a number of site covariates influenced golden mouse occupancy (Table 3). Illinois sites had higher golden mouse model-averaged occupancy than core sites ( $\psi = 0.927 \pm 0.017$  versus  $\psi = 0.688 \pm 0.153$ ). Golden mouse occupancy increased with increasing vine numbers, but decreased with increasing herbaceous and woody stems. The null occupancy model for *Peromyscus* spp. was the most-supported model, indicating that occupancy was not influenced by habitat variables we measured (Table 3). However, larger tree diameter (–), increasing vine numbers (–), and greater canopy cover (+) models were within 2 AIC<sub>c</sub> values, suggesting minor influence of habitat variables on occupancy of *Peromyscus* spp.

The addition of *Peromyscus* spp. as a variable did not improve the fit of co-occupancy models for golden mice (Table 4), suggesting a stronger effect of habitat than of species interactions. Also, based on occupancy modeling, golden mice and *Peromyscus* spp. co-occurred randomly at the sites

**TABLE 2.**—Evaluation of survey covariates, in the 90% model weight ( $w$ ) confidence set, related to per survey detection probability ( $p$ ) for golden mice and *Peromyscus leucopus* in Illinois and *P. leucopus* and *P. gossypinus* in the core of golden mouse geographic range. Null  $p$  model is included to assess relative support of top  $p$  model. We held occupancy constant ( $\psi(\cdot)$ ) and fit encounter history data from surveys at 48 sites in 2008–2009 to the candidate model sets to estimate  $p$ .

Model	AIC <sub>c</sub> <sup>a</sup>	$\Delta$ AIC <sub>c</sub>	$w^b$	$K^c$	Deviance <sup>d</sup>
Golden mice					
(REG + PDET + DATE)	421.27	0.00	0.62	5	410.60
(REG + PDET + DATE + SURVEY)	423.28	2.01	0.23	6	410.34
(REG + PDET + SURVEY)	424.47	3.20	0.12	5	413.80
(.) <sup>e</sup>	500.07	78.80	0.00	2	495.94
<i>Peromyscus</i> spp. <sup>f</sup>					
(REG + PDET + DATE)	541.86	0.00	0.59	5	531.19
(REG + PDET + DATE + SURVEY)	543.92	2.06	0.21	6	530.98
(REG + PDET + SURVEY)	544.53	2.67	0.15	5	533.86
(.) <sup>e</sup>	629.12	87.26	0.00	2	624.99

<sup>a</sup> Akaike information criterion for small samples.

<sup>b</sup> Model probability.

<sup>c</sup> Number of model parameters.

<sup>d</sup> Difference in  $-2 \log(\text{likelihood})$  of the current model and  $-2 \log(\text{likelihood})$  of the saturated model.

<sup>e</sup> Null, constant detection probability.

<sup>f</sup> White-footed mice and cotton mice were combined as ecological equivalents. See “Materials and Methods.”

**TABLE 3.**—Habitat occupancy ( $\psi$ ) model selection results, in the 90% model weight ( $w$ ) confidence set, for golden mice and *Peromyscus leucopus* in Illinois and *P. leucopus* and *P. gossypinus* in the core of golden mouse range. We fit encounter history data from surveys at 48 sites in 2008–2009 to the candidate model sets. The null  $\psi$  model (occupancy held constant for all sites) is included to assess relative support for top  $\psi$  model. For all models, probability of detection ( $p$ ) was held as the most-parsimonious model from stage 1 of the modeling procedure (Table 2).

Model	AIC <sub>c</sub> <sup>a</sup>	$\Delta$ AIC <sub>c</sub>	$w^b$	$K^c$	Deviance <sup>d</sup>
Golden mice					
(REG + VINE + WSTEM)	416.06	0.00	0.17	8	398.40
(REG + VINE + WSTEM + HSTEM)	416.79	0.73	0.12	9	396.70
(WSTEM)	416.90	0.84	0.11	6	403.96
(VINE)	416.95	0.89	0.11	6	404.01
(WSTEM + DBH)	417.48	1.42	0.08	7	402.21
(REG + VINE + WSTEM + HSTEM + CANOPY)	417.70	1.64	0.07	10	395.11
(REG + VINE)	417.79	1.73	0.07	7	402.52
(REG + CANOPY)	418.38	2.32	0.05	7	403.11
(DBH + CANOPY)	418.57	2.51	0.05	7	403.30
(HSTEM + WSTEM)	419.18	3.12	0.04	7	403.91
(REG + VINE + WSTEM + HSTEM + DBH + CANOPY)	419.38	3.32	0.03	11	394.24
(.) <sup>e</sup>	421.27	5.21	0.01	5	410.60
<i>Peromyscus</i> spp. <sup>f</sup>					
(.) <sup>e</sup>	541.86	0.00	0.25	5	531.19
(DBH)	542.86	1.00	0.15	6	529.92
(VINE)	543.27	1.41	0.13	6	530.33
(CANOPY)	543.76	1.90	0.10	6	530.82
(DBH + VINE)	543.97	2.11	0.09	7	528.70
(REG + VINE + WSTEM + HSTEM + CANOPY + DBH)	544.67	2.81	0.06	11	519.53
(DBH + CANOPY)	544.96	3.10	0.05	7	529.69
(DBH + WSTEM)	545.18	3.32	0.05	7	529.91
(WSTEM + HSTEM)	545.25	3.39	0.05	7	529.98

<sup>a</sup> Akaike information criterion for small samples.

<sup>b</sup> Model probability.

<sup>c</sup> Number of model parameters.

<sup>d</sup> Difference in  $-2 \log(\text{likelihood})$  of the current model and  $-2 \log(\text{likelihood})$  of the saturated model.

<sup>e</sup> Null, constant occupancy probability.

<sup>f</sup> White-footed mice and cotton mice were combined as ecological equivalents. See “Materials and Methods.”

surveyed ( $\phi = 1.050 \pm 0.106$ ), suggesting that *Peromyscus* spp. had no influence on the occurrence of golden mice.

## DISCUSSION

A primary assumption of the abundant-center hypothesis is that the edges of a species' range constitute suboptimal habitat. Aspects of climate, resources, interspecific competitors, and predators at the edge combine to be limiting—otherwise the range would extend farther. Despite its intuitive appeal, however, empirical data for the abundant-center hypothesis are equivocal. We found that abundance of golden mice at the periphery of their range in southern Illinois appeared to be greater than in the core of the range. Lack of support in our study for the abundant-center concept parallels other previous work. Fuller et al. (2009) examined 115 studies of 30 primate species and found no support for the center–edge abundance relationship; neither did Stevens et al. (2004) for 3 abundant bat species in Paraguay. Considering a variety of plant and animal taxa, Sagarin and Gaines (2002) examined 22 data sets involving 145 tests of the hypothesis. Although most of the data sets were nonmammalian, they found that only 56 (39%) supported the concept. Numerous other hypotheses have been generated from the abundant-center concept—including the

expectation of larger body size of a species in the core range relative to the edge because of better resource availability. However, Meiri et al. (2009) found no consistent relationship between body size and geographic position on the core–edge gradient for 25 species of mammalian carnivores. Virgós et al. (2011) examined size variation in European badgers (*Meles meles*) and found “mixed support” for the abundant-center hypothesis. Conversely, Yackulic et al. (2011) generated models for 43 large mammalian species and concluded that core populations were less vulnerable to extinction, presumably because of higher densities than edge populations.

Equivocal support for the abundant-center hypothesis may result because a mosaic of interrelated factors affects mammalian species density, including resource availability, habitat structure, interspecific competitors, parasites, predators, and tolerance to anthropogenic influences—factors that all vary temporally on a local scale. For example, Stevens et al. (2004) suggested that species in relatively harsh (edge) areas may have higher densities because fewer competitors can persist there. Few investigators can sample a species range-wide for a prolonged period; abundant-center and other landscape-level relationships may become more tenuous because of the short-term variability of factors affecting species density.

**TABLE 4.**—Co-occurrence model selection results for golden mice habitat models with and without the inclusion of *Peromyscus* spp.<sup>a</sup> occupancy. We fit encounter history data from surveys at 24 sites in Illinois and 24 sites in the core of golden mouse geographic range to the candidate model set.

Model	AIC <sub>c</sub> <sup>b</sup>	ΔAIC <sub>c</sub>	w <sup>c</sup>	K <sup>d</sup>	Deviance <sup>e</sup>
(VINE + WSTEM)	1,031.17	0.00	0.27	12	1,003.41
(REG + VINE)	1,031.30	0.13	0.25	12	1,003.54
(VINE)	1,031.32	0.15	0.25	11	1,006.18
(REG + VINE + WSTEM)	1,032.32	1.15	0.15	13	1,001.88
(REG)	1,035.46	4.29	0.03	11	1,010.32
(REG + <i>Peromyscus</i> spp.)	1,035.59	4.42	0.03	12	1,007.83
(WSTEM)	1,036.94	5.77	0.02	11	1,011.80
( <i>Peromyscus</i> spp.)	1,040.50	9.33	0.00	11	1,015.36
(REG + VINE + <i>Peromyscus</i> spp.)	1,041.73	10.56	0.00	13	1,011.29
(REG + VINE + WSTEM + <i>Peromyscus</i> spp.)	1,044.48	13.31	0.00	14	1,011.29
(VINE + WSTEM + <i>Peromyscus</i> spp.)	1,045.25	14.08	0.00	13	1,014.81
(WSTEM + <i>Peromyscus</i> spp.)	1,046.02	14.85	0.00	12	1,017.54

<sup>a</sup> White-footed mice and cotton mice were combined as ecological equivalents. See “Materials and Methods.”

<sup>b</sup> Akaike information criterion for small samples.

<sup>c</sup> Model probability.

<sup>d</sup> Number of model parameters.

<sup>e</sup> Difference in  $-2 \log(\text{likelihood})$  of the current model and  $-2 \log(\text{likelihood})$  of the saturated model.

Three caveats are warranted for our study. First, we sampled all Illinois sites in 2008 and all core sites in 2009 when biotic or abiotic factors may have been less conducive to small mammal capture. Thus, our results for the core area may reflect an anomalous “down year” for small mammal captures, perhaps reflecting decreased population densities because of low mast production the previous year or 2 (Gashwiler 1979; Woolf 1996) or lower capture rates because of higher ambient temperatures. Higher ambient temperatures causing increased metabolic rates and respiratory water loss of mice (Hill 1983) have been associated with reduced foraging and consumption (Sealander 1952). This effect was unlikely on our sites, however, given no difference in mean high temperatures during trapping periods. Considering we caught only 65 *Peromyscus* spp. in the core (44 white-footed mice and 21 cotton mice) during 11,760 trap nights—an extremely low success rate of 0.005 per trap night—makes reduced population size most plausible; we captured 3.75 times more white-footed mice the previous year in Illinois. Second, our study was designed to gather data for a decision on delisting golden mice in Illinois. Thus, only populations in Illinois represent the periphery of the range—we intentionally avoided peripheral sites in the core. Also, the distribution of our 24 core trap sites was limited by time and travel constraints to 7 states. We doubt this influenced overall results, however, because reported densities for golden mice throughout their range are highly variable (Rose 2008:table 3.1). Third, although we caught no golden mice at 11 sites throughout the core of the range, arboreal nests were noted on 3 of these sites and may have been occupied. Thus, the disparity between occupied sites in Illinois versus the core may have been less than our trapping data and occupancy models suggest. Regardless, it is clear that in terms of occupancy and relative abundance, our results indicate that golden mice are at least as common at the periphery of their geographic range in Illinois as in the core.

Several factors may affect occupancy and abundance of golden mice in Illinois and throughout their range, with few landscape-level generalizations possible. For example, densities are highly variable spatially and temporally (Linzey and Packard 1977; Rose 2008). Although sometimes fairly common in localized areas, golden mice generally are uncommon, with population densities less than those of sympatric species of *Peromyscus* (Feldhamer and Morzillo 2008). The reported variation in density may reflect different trapping protocols, but site-specific and seasonal differences may have affected results of our study. Despite reduced captures in the core of the range, however, the percentages of golden mice among total individuals captured were similar—31.6% in the core and 28.9% in Illinois.

The extent of interspecific competition between golden mice and sympatric *Peromyscus* spp. also appears to be highly variable and site-specific. Inverse relationships between abundance of golden mice and *Peromyscus* spp. have been attributed to interspecific competition by several investigators (Feldhamer and Maycroft 1992; Linzey 1968; McCarley 1958; Pearson 1953; Seagle 1985), although different habitat selection may have been operative. Other studies, however, have found no relationship (Christopher and Barrett 2006; Faust et al. 1971). We found that occurrence of white-footed mice or cotton mice at our sites had no influence on probability of occurrence of golden mice. Also, based on occupancy modeling, the species co-occurred randomly at the sites surveyed, again suggesting no positive or negative influence of *Peromyscus* spp. on occupancy or abundance of golden mice. Also, behavioral differences between golden mice and *Peromyscus* spp. may affect perceived occupancy. For example, Feldhamer and Maycroft (1992) found that individual golden mice were relatively “trap shy”—they were trapped significantly fewer times and in fewer traps than sympatric white-footed mice.

Demographic and behavioral factors associated with capture of small mammals are interrelated and often difficult to assess, with conclusions and generalities usually difficult to make (Gaston and Kunin 1997). Nonetheless, although our data do not support the abundant-center hypothesis, from a management standpoint, they support delisting the golden mouse as a state-threatened species in Illinois. As noted, an abundant-center scenario with gradual reduction in population density toward the edges of the geographic range has generated numerous biogeographic, demographic, behavioral, and genetic hypotheses (Sagarin and Gaines 2002), including that extinction is more likely at edges (Lomolino and Channell 1995; Nathan et al. 1996). States may list plant or animal species that occur peripherally as threatened or endangered based on limited data and the implicit assumption—intuitively appealing—that extirpation is more likely at the edge of the range because population abundance presumably is lower and less stable (Brown 1984; Hengeveld and Haeck 1982; Schoener 1987). Our study, and the lack of support for the abundant-center hypothesis for a variety of other taxa (Sagarin and Gaines 2002), suggests caution in acceptance of this basic assumption because it may lead to inappropriate conservation strategies.

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## APPENDIX I

Site number, counties, UTM location, and number of individual golden mice (*Ochrotomys nuttalli*) captured at each trap site in Illinois (IL) from April through October 2008.

Trap site	County	UTM zone	UTM easting	UTM northing	# <i>O. nuttalli</i> round 1	# new <i>O. nuttalli</i> round 2	# <i>O. nuttalli</i> recaptures round 1 to 2
IL-1	Williamson	16S	314606	4173367	2	0	0
IL-2	Williamson	16S	315017	4170825	2	0	2
IL-3	Williamson	16S	314414	4164169	4	2	2
IL-4	Jackson	16S	296751	4166469	1	1	0
IL-5	Jackson	16S	296058	4166481	2	0	0
IL-6	Jackson	16S	297120	4167616	2	0	1
IL-7	Johnson	16S	332104	4158567	7	0	5
IL-8	Johnson	16S	333041	4152919	8	1	2
IL-9	Johnson	16S	333817	4153180	6	3	3
IL-10	Alexander	16S	292513	4127132	6	0	5
IL-11	Alexander	16S	291610	4123541	3	0	2
IL-12	Alexander	16S	293217	4133912	6	0	4
IL-13	Pope	16S	349064	4151442	3	0	1
IL-14	Pope	16S	354804	4155663	1	0	0
IL-15	Pope	16S	356734	4154939	0	0	0
IL-16	Jackson	16S	281880	4184235	12	3	8
IL-17	Jackson	16S	280892	4185103	2	1	4
IL-18	Jackson	16S	278804	4190275	7	3	3
IL-19	Pope	16S	354867	4141070	1	4	1
IL-20	Pope	16S	353900	4142530	0	3	0
IL-21	Pope	16S	358192	4143857	0	0	0
IL-22	Pope	16S	370027	4159992	0	0	0
IL-23	Saline	16S	374230	4170100	2	0	1
IL-24	Gallatin	16S	382218	4163706	0	1	0
				TOTALS	77	22	44

## APPENDIX II

Site number, state\*, counties, UTM location, and number of individual golden mice (*Ochrotomys nuttalli*) captured at each trap site throughout the core of the species range from May through October 2009.

Trap site	County	UTM zone	UTM easting	UTM northing	# new <i>O. nuttalli</i> round 1	# new <i>O. nuttalli</i> round 2	# <i>O. nuttalli</i> recaptures round 1 to 2
AR-1	Montgomery	15S	470931	3822954	2	0	0
AR-2	Montgomery	15S	447814	3819322	1	1	0
AR-3	Montgomery	15S	454939	3821189	2	0	0
MS-1	Marshall	16S	282638	3835322	0	0	0
MS-2	Marshall	16S	290683	3831371	5	1	3
MS-3	Marshall	16S	280439	3830299	2	1	2
AL-1	Talladega	16S	580688	3673319	0	0	0
AL-2	Talladega	16S	583215	3680345	0	2	0
AL-3	Talladega	16S	583681	3684327	0	1	0
AL-4	Lawrence	16S	465576	3801118	0	0	0
AL-5	Lawrence	16S	467134	3798798	0	0	0
AL-6	Lawrence	16S	467428	3798996	0	0	0
FL-1	Liberty	16R	742451	3353762	1	0	0
FL-2	Liberty	16R	737952	3327104	0	0	0
FL-3	Liberty	16R	741134	3360125	0	1	0
GA-1	Greene	17S	265106	3675393	1	1	0
GA-2	Greene	17S	257298	3671790	2	0	0
GA-3	Greene	17S	256615	3672093	0	0	0
SC-1	Newberry	17S	435114	3808778	0	0	0
SC-2	Newberry	17S	433247	3814721	1	1	1
SC-3	Newberry	17S	434065	3818427	4	0	1
TN-1	Pickett	16S	706964	4038142	0	0	0
TN-2	Pickett	16S	689272	4048021	0	0	0
TN-3	Pickett	16S	697908	4047287	0	0	0
				TOTALS	21	9	7

\* AL – Alabama; AR – Arkansas; FL – Florida; GA – Georgia; MS – Mississippi; SC – South Carolina; TN – Tennessee.