Mammalia 74 (2010): 379–393 © 2010 by Walter de Gruyter • Berlin • New York. DOI 10.1515/MAMM.2010.052

Habitat use and demographic characteristics of the west Mexican cotton rat (*Sigmodon mascotensis*)

Gary D. Schnell[1,*], María de Lourdes Romero-Almaraz[2], Sara T. Martínez-Chapital[3], Cornelio Sánchez-Hernández[3], Michael L. Kennedy[4], Troy L. Best[5], Michael C. Wooten[5] and Robert D. Owen[6]

[1] Sam Noble Oklahoma Museum of Natural History and Department of Zoology, 2401 Chautauqua Avenue, University of Oklahoma, Norman, OK 73072, USA, e-mail: gschnell@ou.edu
[2] Escuinapa No. 92 bis. Col. Pedregal de Santo Domingo, C.P. 04360, México, D.F., México
[3] Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, Coyoacán, México, D.F. 04510, México
[4] Ecological Research Center, Department of Biology, University of Memphis, Memphis, TN 38152, USA
[5] Department of Biological Sciences, 331 Funchess Hall, Auburn University, AL 36849, USA
[6] Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA, and Martín Barrios 2230 c/Pizarro, Barrio Republicano, Asunción, Paraguay

*Corresponding author

Abstract

In tropical deciduous forest along the Pacific coast in Colima, Mexico, we conducted eight-night mark-recapture studies of *Sigmodon mascotensis* (January 2003–2005), evaluating habitat preferences and demography. Yearly we established five grids with 100 trapping stations (one ground and one elevated trap; 24,000 trap-nights), each evaluated for 14 environmental measures. We captured 96 *S. mascotensis* 274 times on 10 grids, most at ground level (85.6%), with densities of 0.84–25.31 individuals/ha. Adults predominated (88.2%), sex ratio (males:females) was 1:0.74, and males were heavier. *Sigmodon mascotensis* co-occurred with *Oryzomys couesi* and *Baiomys musculus* more often and *Heteromys pictus* less often than chance expectation. For 2004, univariate analyses indicated that stations frequented had more ground cover in woody plants, forbs and grasses; less in litter and bare ground; more vegetation low and less high; lower and more open canopy; and longer distance to nearest tree. Logistic regression indicated preference for open canopy, dense low vegetation, little litter and longer distance to nearest tree. Nonparametric multiplicative regression showed occurrence likelihood decreased as litter increased and increased with increasing slope, average hits at 1 m and average distance to nearest tree. The likelihood was high with no or low canopy, as well as high canopy.

Keywords: Colima; Cricetidae; density; HyperNiche; logistic regression.

Introduction

The west Mexican cotton rat (*Sigmodon mascotensis* Allen 1897) occurs in western Mexico from southern Nayarit and southwestern Zacatecas south to southwestern Chiapas, and as far east as western Hidalgo, western Puebla and northwestern Oaxaca (Musser and Carleton 2005). Detailed information on the ecology of *S. mascotensis* is sparse, with most studies mentioning the species only in passing. In addition, some potentially relevant studies of cotton rats conducted within the geographic range of *S. mascotensis* were completed when the systematic status of the species was unclear (Barrera 1952, Baker and Greer 1962).

The species occurs from sea level to 2550 m (Juárez Gómez 1992, Carleton et al. 1999) in a variety of natural habitats, as well as in agricultural areas. It is associated with habitats moist enough to support grass, which provides food and cover, retards evaporation and decreases ambient temperature (Stickel and Stickel 1949, Baker 1969, Zimmerman 1970). Carleton et al. (1999) noted that ''the occurrence of the species corresponds closely to deciduous and semideciduous woodlands having a pronounced dry season''. *Sigmodon mascotensis* makes runways through vegetation and is active day and night (Zimmerman 1970, Miranda 2002b). Some investigators have suggested that high densities of this species in cropland make them a potential plague (Ceballos and Miranda 1986, 2000), but Barrera (1952) stated that they do not cause significant damage to crops because, although they tend to nibble on agricultural plants, their main food is seeds of wild grasses.

We investigated the ecology and demography of *Sigmodon mascotensis* during the dry season at a coastal location in Colima, Mexico, with objectives being: to analyze demographic parameters such as density, sex ratio and age structure; to evaluate reproductive condition and size of individuals; to acquire information on relative movement by males and females; to discern co-occurring species; to estimate probability of capture; and to evaluate habitat use based on vegetation-structure variables.

Materials and methods

Study area

Our investigation was conducted at Playa de Oro (19°08′ N, 104°31′ W), municipality of Manzanillo, in Colima, Mexico

(Figure 1). The study area was less than 1 km from the Pacific Ocean, elevation was less than 10 m above sea level and topography generally was flat. The habitat was primarily tropical dry deciduous forest, with thorn forest and mangrove elements. Common trees and shrubs included *Coccoloba barbadensis* Jacq., several species of *Acacia* [including *Acacia hindis* Benth. and *Acacia farnesiana* (L.)], *Senna pallida* (Vahl) H.S. Irwin and Barneby, *Senna occidentalis* (L.) Link, *Pithecellobium lanceolatum* (Willd.) Benth., *Pithecellobium dulce* (Roxb.) Benth., *Hyperbaena ilicifolia* Standl., *Crataeva tapia* L., *Prosopis juliflora* (Sw.) DC., and *Guazuma ulmifolia* Lam. (Schnell et al. 2008a,b). The area was exposed to grazing by livestock, but large areas were not accessible to livestock owing to the density of vegetation. Much of the adjacent area was used for agriculture, including production of corn (*Zea mays* L.), sweet potatoes [*Ipomoea batata* (L.) Lam.], beans (*Phaseolus vulgaris* L.) and coconut palms (*Cocos nucifera* L.).

The study was conducted on 1–13 January in 2003, 2004 and 2005. Average temperature for January for Manzanillo, 21 km east-southeast from the study site, was 24.6°C with a monthly rainfall of 31.3 mm (average 1961–2005; Instituto Nacional de Estadística, Geografía e Informática 2006).

Trapping

Each year we established five 1-ha trap grids (15 grids total for the 3 years). Locations each year were such that the grids covered the various types of vegetation in the vicinity (thorn forest, overgrown plantation of coconut palms, mangrove forest and relatively open grassy areas; Table 1). Each grid had 100 trapping stations (10×10), with adjacent stations 10 m apart. Each station had two Sherman live traps (7.5×9.0×23.0 cm; H.B. Sherman Traps, Tallahassee, FL, USA). One trap was on the ground and another 1–3 m above ground on a thin plywood platform (12.5×34.5 cm) attached to a tree or shrub (hereafter referred to as an arboreal trap); both were baited with rolled oats.

Most grids were sampled for 8 nights (Table 1). Exceptions were grid 5 in 2004 (9 nights) and grid 1 in 2005 (7 nights). The overall sampling effort on grids involved 24,000 trap-nights (1 trap-night=1 trap set for 1 night). Traps were checked each morning, re-baited as needed and opened for the full 24-h period.

For each *Sigmodon mascotensis* caught, we recorded trap position (i.e., grid location and whether in a ground or arboreal trap), sex, reproductive condition (i.e., judged reproductively active or not, depending on external condition of reproductive organs) and age (adult, subadult or juvenile based on size, mass, reproductive condition and pelage coloration). Adults have a pale cinnamon back, darker along the midline and paler on sides and a white belly; juveniles have a yellowish tawny brown back and a soiled buffy gray belly (Allen 1897, Ramírez and Chávez Tovar 2005). Subadults and juveniles are similar in coloration. In general, juveniles had a total length less than 160 mm and subadults less than 200 mm. Animals were tagged in both ears using numbered Monel No. 1 ear tags (National Band and Tag Company, Newport, KY, USA) and released at the site of capture.

Estimation of movement, abundance and density

For each *Sigmodon mascotensis* captured more than once, we determined the average distance from the centroid of its

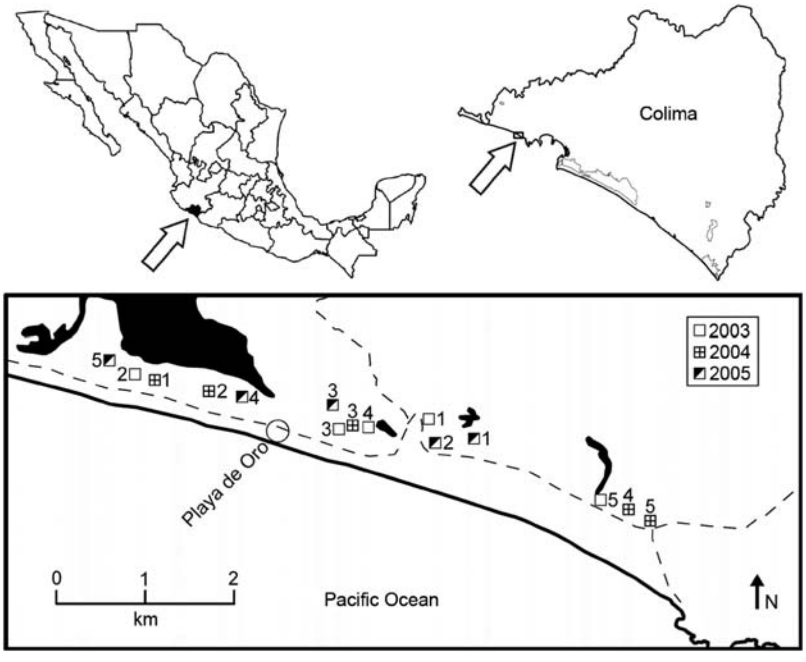

Figure 1 Upper left panel shows location of state of Colima in Mexico and upper right panel the location of Playa de Oro in Colima. Lower panel depicts location of grids in vicinity of Play de Oro, with specific grids designated by numbers. Darkened areas indicate extent of lagoons and marshes, and dashed lines denote roads and trails.

Table 1 Brief description of vegetation of each grid used in study of *Sigmodon mascotensis* in Playa de Oro, Colima, Mexico, with sampling dates indicated (descriptions modified from Schnell et al. 2008b).

Grid number (January dates)	Description
2003	
1 (2–5, 9–12)	Thorn forest with some palm trees close to mangroves
2 (2–5, 9–12)	Thorn forest with some palm trees close to mangroves
3 (3–5, 9–13)	Thorn forest next to palm plantation
4 (3–5, 9–13)	Thorn forest next to palm plantation
5 (3–5, 9–13)	Mix of grassy plots and palm trees associated with undergrowth of thorn forest
2004	
1 (3–5, 9–13)	Mixture of thorn forest and mangrove, with some palm trees
2 (2–5, 9–12)	Mixture of thorn forest and mangrove, with some palm trees
3 (2–5, 9–12)	Thorn forest close to palm plantation
4 (3–5, 9–13)	Mixture of grassy plots, palm trees and thorn forest next to agricultural fields
5 (2–5, 9–13)	Mixture of grassy plots, palm trees and thorn forest next to agricultural fields
2005	
1 (4–6, 10–13)	Dense thorn forest with abundance of woody vines
2 (3–6, 10–13)	Thorn forest mixed with mangrove and palm trees with dense undergrowth
3 (2–6, 10–12)	Mixture of thorn forest, grassy plots and xerophilous shrubs
4 (2–6, 10–12)	Mixture of grassy plots, palm trees associated with dense undergrowth of thorn forest, and patches of mangrove
5 (3–6, 10–13)	Mixture of grassy plots, palm trees and thorn forest

capture sites (for animals caught two or more times, but always at the same trapping station, the resulting distance was 0 m). This approach to evaluating movements is related to the center-of-activity concept proposed by Hayne (1949) and employed in a study of the southern pygmy mouse [*Baiomys musculus* (Merriam 1892); Schnell et al. 2008b]. For individuals captured more than once, we also determined the distance between successive captures (Slade and Swihart 1983). This measure was calculated weighting each individual equally, as well as weighting each occurrence equally (e.g., for the latter, an individual caught seven times would contribute six data points and one caught two times would provide one).

We used two models in the computer program MARK (White and Burnham 1999, White 2007) to estimate the abundance of *Sigmodon mascotensis* on grids and the probability of capture on a given night. Based on the assumption of a closed population during the trapping period (Otis et al. 1978), relative proportions of marked and unmarked animals in successive samples were compared to estimate abundance, with parameters modeled as functions of each other. Probability of capture (p) and recapture (c) were employed to estimate abundance (N) for a given grid. Both models we used can be designated by $p(t)=c(t)$, where p and c were modeled as equal, but could vary with time (t; i.e., night). The difference was that in Model 1 the values were estimated as being the same for all grids, whereas in Model 2 the values could vary among grids. Models were compared using the Akaike information criterion as modified to adjust for small-sample bias (AIC_c; White 2007).

Abundance values for a grid can be converted into densities given an estimate of the effective grid area. To estimate area at the edge of the grid, we used average distance from centroid of trapping stations where animals were caught, weighting individuals equally. This average value was added to each side of the central portion (i.e., 8100 m^2; 90×90 m) of the grid; we considered corners of the effective grid area to be rounded with a radius equal to average distance from centroid. Density estimates (individuals/ha) were obtained by dividing abundance values from MARK by the resulting effective grid area (i.e., 1.195 ha based on distance-from-centroid values reported in the results section).

Structure of vegetation

In 2004 we quantified 14 vegetation-structure variables (Table 2) following Schnell et al. (2008a,b). Measurements were made adjacent (i.e., approximately 1 m west) to each trapping station (100 points/grid; 500 points total). The percentage ground cover was estimated to the nearest 5% for a 1-m square (variables 1–7 in Table 2). The number of shrub stems hitting a 1-m bar at 1-m height was determined four times (once in each cardinal direction from the central point) and the average calculated (variable 8). Canopy cover (i.e., percent closed, variable 9) was estimated using a spherical densitometer (model C, Forest Densitometers, Bartlesville, OK, USA) and slope (variable 10) using a clinometer. With a 7.5-m vertical pole marked at each decimeter, we determined the number of decimeter intervals touched by vegetation; resulting data were summed for 0–2.5 m (maximum of 25 hits; variable 11) and 2.5–7.5 m (maximum 50; variable 12). We estimated maximum height of canopy to the nearest 0.5 m (variable 13). The distance to nearest tree greater than 10 cm in diameter at breast height (dbh) was determined in each of four quadrants (with edges being the cardinal directions) and the average calculated (distances $\geq$10 m were tabulated as 10 m; variable 14).

Table 2 Mean±SD (range) of 14 independent variables measured to provide quantitative assessment of vegetation structure on trap grids used to ascertain habitat preferences, contrasting trapping stations where *Sigmodon mascotensis* was captured and not captured in 2004 at Playa de Oro, Colima, Mexico.

Variable	Trapping stations where	
	Captured (n=125)	Not captured (n=375)
1. Percent woody plants	9.6±16.3 (0–95)*	6.8±10.0 (0–65)
2. Percent forbs	15.8±26.6 (0–95)***	7.9±15.2 (0–95)
3. Percent grasses	22.0±32.8 (0–100)***	8.0±21.1 (0–100)
4. Percent litter	20.0±20.2 (10–90)***	37.1±26.9 (0–95)
5. Percent dead wood	12.7±18.2 (0–85)	15.3±14.9 (0–90)
6. Percent rocks	0.0±0.4 (0–5)	0.2±1.2 (0–10)
7. Percent bare ground	19.9±22.3 (0–80)*	24.7±23.4 (0–90)
8. Average hits at 1 m	1.4±1.8 (0–10)***	0.6±0.9 (0–7)
9. Percent canopy closed	49.3±42.5 (16.8–100.0)***	80.1±29.9 (0.2–100.0)
10. Slope (degrees)	3.9±4.4 (0–10)	3.3±3.8 (0–17)
11. Total hits low (0.0–2.5 m)	4.7±4.1 (0–25)***	3.2±3.3 (0–16)
12. Total hits high (2.5–7.5 m)	1.8±3.9 (0–30)***	3.8±4.3 (0–39)
13. Maximum canopy height (m)	5.1±4.4 (2.5–20.0)***	7.8±3.9 (0.0–20.0)
14. Average distance to nearest tree (m)	6.5±2.8 (1.75–10.00)***	4.7±2.4 (0.75–10.00)

Asterisks indicate statistical differences between stations where *S. mascotensis* was captured and not captured (one-way ANOVA): *$p<0.05$; **$p<0.01$; ***$p<0.001$; no symbol, $p>0.05$.

Logistic regression and nonparametric multiplicative regression

Given that many more *Sigmodon mascotensis* were captured in 2004 than in 2003 or 2005, we restricted our quantitative assessments of habitat use to data from 2004. With stepwise logistic regression (Systat 12; Systat Software 2007), we examined vegetation structure at trapping stations where *S. mascotensis* was captured (n=125) one or more times and contrasted these with stations where the species was not captured (n=375) on any of the 8 nights sampled. The dependent variable was logit (*Y*), which is the natural logarithm of the probability of the species being present, and the 14 vegetation-structure variables were potential independent variables. Significance to include or remove a variable was set at 0.05. McFadden's ρ^2-statistic, which varies from 0–1, was used to evaluate resulting models as a whole. It is a transformation of a likelihood-ratio statistic intended to mimic R^2, with higher values indicating more significant results. The ρ^2-values tend to be lower than R^2-values (0.20–0.40 have been considered satisfactory), and low values do not necessarily indicate poor fit of the model (Systat Software 2007).

We also used nonparametric multiplicative regression (NPMR) as implemented in the program HyperNiche (version 1.46; McCune and Mefford 2004) to model habitat occupied by *Sigmodon mascotensis* based on the same data. NPMR creates habitat models in which predictor variables are combined multiplicatively rather than additively and where the overall form of response surfaces need not be specified in advance. Thus, the response of a species to environmental variables could be linear, but procedures also accommodate, e.g., responses in the form of normal or bimodal distributions. NPMR does not produce coefficients in a mathematical equation, but rather optimizes data fit without reference to a specific global model, producing graphical representations of response curves and surfaces.

One chooses a local model that specifies shape of the function to be used to fit a value for a specific point in the space defined by predictor variables, as well as a kernel function specifying how local is ''local'' (McCune 2006). NPMR uses a local multiplicative smoothing function, with leave-one-out cross-validation, to estimate the response variable (Berryman and McCune 2006) and to select an appropriate weighting parameter for the kernel function. In HyperNiche, we used the local-mean model type, where weighting around each target point or kernel is based on a Gaussian (hump-backed) function.

We conducted an exhaustive free search for the best model, where all combinations of the 14 variables (one at a time, two at a time, etc.) and tolerances (i.e., SDs used in Gaussian smoothers) were evaluated until no improvement in fit was achieved. We used xR^2, which assesses the cross-validated residual sum of squares in relation to total sum of squares, as a measure of model fit. It differs from R^2 in that each data point is excluded from the basis for estimating the response at that point (McCune 2006). After the exhaustive search, we selected the best model for variables taken one at a time, two at a time, etc., and compared these ''best'' models using xR^2. Based in large part on degree of improvement in fit per variable added, we selected the best overall model for predicting the likelihood of occurrence of *Sigmodon mascotensis*.

Other statistical analyses

We employed BIOMstat for Windows 3.30s (Rohlf and Slice 1999) to conduct a variety of univariate analyses. These included the R×C test, goodness-of-fit test and Fisher's exact test for analysis of frequencies, and one-way analysis of variance (ANOVA) in assessment of continuous variables.

Results

Demographic characteristics

During the 3-year study, 96 individual *Sigmodon mascotensis* were captured. Animals were recaptured 178 times, giving a total of 274 captures and recaptures during 24,000 trap-nights. Most individuals were caught in ground-level traps (231 of 270 captures for which the specific trap was recorded; 85.6%). During 2003 and 2005, only four and eight individuals were trapped, respectively, whereas in 2004, 84 were captured with the same trapping effort. No individual was recorded moving between grids.

We recorded age of 93 of the 96 *Sigmodon mascotensis* with 82 being adults (88.2%), eight juveniles (8.6%) and three subadults (3.2%). All in 2003 (four individuals) and 2005 (seven) were adults, whereas in 2004, 71 of 82 individuals were adults (86.6%). Each year more adult males than females were trapped: 2003, three males (75%) and one female (25%); 2004, 40 males (56.3%) and 31 females (43.7%); and 2005, four males (57.1%) and three females (42.9%). The 47 males (57.3%) and 35 females (42.7%) for all years give a male:female ratio of 1:0.74, which is not significantly deviant from 1:1 (goodness-of-fit test, $G=1.76$, $df=1$, $p=0.184$).

We noted reproductive condition for 26 adult females and 34 adult males. The majority of adult females during the 3 years were reproductively inactive (14 of 26, 53.8%). Reproductive condition was not registered for the only female caught in 2003. In 2004, 11 of 23 adult females were inactive (47.8%), five were lactating (21.7%), four were postlactating (17.4%), one was pregnant (4.3%) and two had an open vagina (8.7%). For 2005, all three females were reproductively inactive. Most adult males caught had abdominal testes (22 of 34, 64.7%). For 2003, the condition of three adult males was recorded, one having abdominal testes (33.3%) and two having inguinal testes (66.7%). For 2004, 18 of 27 adult males had abdominal testes (66.7%), one had inguinal testes (3.7%) and eight had scrotal testes (29.6%). For 2005, four adult males were caught, three with abdominal testes (75.0%) and one with scrotal testes (25.0%).

There was a significant difference in mass between adult males and females (one-way ANOVA; $F_{1,79}=3.97$, $p=0.049$), with males being heavier. Means and SDs were 104.32±27.71 g (n=47, range 49.3–168.0 g) for males and 92.08±26.67 g (n=34, range 43.9–160.0 g) for females.

Average distance from centroid for capture sites of adults was obtained for 62 *Sigmodon mascotensis* (three in 2003, 54 in 2004 and five in 2005) based on from two to seven recaptures per animal. There was no evidence of differences among years, so data for the 3 years were pooled. For adult males the average distance from centroid was 9.97±6.60 m (n=35, range 0–25.49 m) and for adult females 9.69±9.60 m (n=27, range 0–46.53 m). There was no significant difference between sexes (one-way ANOVA; $F_{1,60}=0.02$, $p=0.893$). Combining all data for *S. mascotensis*, irrespective of sex or age, average distance from centroid was 9.85±7.97 m (n=62, range 0–46.5 m). To estimate the effective area of a grid, this average was added to each side of the central portion of the grid (90×90 m), and corners were estimated as having an equivalent radius, resulting in an effective grid area of 1.195 ha.

Giving equal weight to individual *Sigmodon mascotensis*, the average distances between successive captures for males and females were similar (males 15.13±11.75 m, n=35, range 0.0–51.0 m; females 15.35±14.64 m, n=27, range 0.0–68.2 m). For sexes combined, the average was 15.22±12.97 m (n=62, range 0.0–68.2 m). When giving equal weight to each occurrence, males averaged 15.87±13.74 m (n=91, range 0.0–70.7 m) and females 15.84±18.00 (n=69, range 0.0–114.0). Clearly, no difference was evident between sexes; the average for pooled data was 15.85±15.74 m (n=160, 0.0–114.0 m).

We captured *Sigmodon mascotensis* on 10 of 15 grids, with the number of individuals ranging from one to 29. For grids in 2003 and 2005, densities were low, and program MARK was not able to provide a robust estimate of total number of animals present. Therefore, we used number of individuals captured as our estimate of number present to obtain the following estimates of density: 2003, grid 1, three animals (2.51 individuals/ha); 2003, grid 4, one (0.84/ha); 2005, grid 1, four (3.35/ha); 2005, grid 2, one (0.84/ha); and 2005, grid 4, three (2.51/ha). For grids in 2004, we used two models to estimate density; both considered probability of capture and recapture equal for a given night. For Model 1, where values were constrained to be the same for all grids, abundances on different grids were 3.00–30.61 individuals/grid, which convert to density estimates of 2.51–25.62/ha (Table 3). Based on Model 2, where values were allowed to differ among grids, estimates were 3.00–30.24/grid, resulting in densities of 2.51–25.31/ha (Table 3). Given calculated AIC_c-values (490.10 for Model 1, 446.22 for Model 2), Model 2 was judged to produce more reliable results.

Co-occurring species

Number of individuals of *Sigmodon mascotensis* and total number of small mammals caught each year on grids were: 2003, four of 286 (1.4%); 2004, 84 of 551 (15.2%); 2005, eight of 206 (3.9%); and all years, 96 of 1043 (9.2%). There was a significant difference among years in percentage of captured animals that were *S. mascotensis* (R×C test; $G=60.65$, $df=2$, $p<0.001$). In 2004, *S. mascotensis* made up a higher percentage of total animals caught. Comparing years, one nonsignificant subset was identified (2003 and 2005), indicating that for these years percentages of *S. mascotensis* could not be differentiated statistically.

The most abundant species of small mammal at Playa de Oro was *Oryzomys couesi* (Alston 1877) (Coues' oryzomys) with 569 of 1043 individuals captured (54.6%). Other common species were *Baiomys musculus* (135, 12.9%; see Schnell et al. 2008b) and *Heteromys pictus* (Thomas 1893) (painted spiny pocket mouse; 106, 10.2%), and their numbers were larger than for *Sigmodon mascotensis*. Species with lower percentages were *Heteromys spectabilis* (Genoways 1971) (Jaliscan spiny pocket mouse), *Nyctomys sumichrasti* (Saussure 1860) (Sumichrast's vesper rat), *Osgoodomys banderanus* (Allen 1897) (Osgood's deer-

Table 3 Total numbers of individuals captured, estimates (*N*) of number of animals on grids using MARK, and estimates of densities of *Sigmodon mascotensis* on individual grids for 2004, at Playa de Oro, Colima, Mexico, based on two models involving $p(t)=c(t)$, where probabilities of capture (p) and recapture (c) are equal for a given night (t), but can vary among nights: (Model 1) values same for all grids; and (Model 2) values estimated separately for each grid.

Grid	No. animals captured	Model 1: $p(t)=c(t)$, same for all grids		Model 2: $p(t)=c(t)$, each grid estimated separately	
		N±SE (95% confidence interval)	Density	N±SE (95% confidence interval)	Density
1	17	17.00±0.000 (17.00–17.00)	14.23	17.00±0.000 (17.00–17.00)	14.23
2	9	9.00±0.000 (9.00–9.00)	7.53	9.00±0.002 (9.00–9.00)	7.53
3	3	3.00	2.51	3.00	2.51
4	25	25.40±1.043 (25.03–31.59)	21.26	26.05±1.503 (25.13–33.32)	21.80
5	30	30.61±1.143 (30.06–36.76)	25.62	30.24±0.993 (30.01–36.75)	25.31

With only three individuals caught on grid 3, program MARK was not able to provide a robust density estimate, so number trapped was used as estimate of number present.

mouse), *Oligoryzomys fulvescens* (Saussure 1860) (fulvous colilargo), *Peromyscus perfulvus* (Osgood 1945) (tawny deermouse; *see* Schnell et al. 2008a), *Reithrodontomys fulvescens* (Allen 1894) (fulvous harvest mouse), *Xenomys nelsoni* (Merriam 1892) (Magdalena woodrat) and *Tlacuatzin canescens* (Allen 1893) (gray mouse opossum).

Given equal sampling with arboreal and ground traps, *Sigmodon mascotensis* was caught predominantly on the ground. Other highly terrestrial species encountered on grids were *Baiomys musculus*, *Heteromys pictus* and *Heteromys spectabilis*; all were caught at one or more of the same trapping stations as *S. mascotensis*. Arboreal and semiarboreal species included *Nyctomys sumichrasti*, *Osgoodomys banderanus*, *Oligoryzomys fulvescens*, *Peromyscus perfulvus*, *Reithrodontomys fulvescens*, *Xenomys nelsoni*, *Oryzomys couesi* and *Tlacuatzin canescens*. Of these, four (*P. perfulvus, R. fulvescens, O. couesi* and *T. canescens*) were caught at one or more of the same trapping stations as *S. mascotensis*.

In 2004, *Sigmodon mascotensis* was substantially more abundant than in other years, being captured at 125 of the 500 trapping stations. Nine other species were obtained at trapping stations that year, including seven that were trapped at more than 10 stations (Table 4). Using Fisher's exact test, these were evaluated as to whether they shared trapping stations with *S. mascotensis* more or less often than expected simply by chance. *Oryzomys couesi*, the most abundant species on grids in 2004, shared more stations than expected by chance (102 versus the expected 75.3; Table 4), with the deviation being highly significantly different from expectation. Also, a highly significant positive association occurred between *S. mascotensis* and *Baiomys musculus*, with the two species sharing almost twice as many stations as predicted on the basis of chance alone (Table 4). One species, *Heteromys pictus*, shared significantly fewer trapping stations with *S. mascotensis* than predicted by chance; thus, although they shared grids, these species were using different places on grids. Three species, *Peromyscus perfulvus, Reithrodontomys fulvescens* and *Heteromys spectabilis*, shared fewer stations with *S. mascotensis* than chance would predict, but deviations were less substantial and did not reach statistical significance. *Tlacuatzin canescens* shared four sites with *S. mascotensis*, exactly the number predicted by chance alone.

Probability of capture

Three grids in 2004 had sufficient numbers of captures to estimate nightly probability of capture using Model 2. For grids 1 and 5, probability of capture increased substantially for the first 6 nights each was trapped, followed by a leveling off on the seventh night and a drop on the last night (Figure 2). On grid 4, the initial probability of capture was higher (>0.3) and increased through the first 4 nights of trapping, after which it steadily decreased to 0 on the last night.

Ecological characteristics comparing trapping stations

For 2004 we used one-way ANOVA to contrast trapping stations for each of the 14 vegetation-structure measurements, comparing the 125 stations where *Sigmodon mascotensis* was caught and the 375 where it was not caught. Significant differences were detected for 11 of 14 variables (Table 2). Stations where *S. mascotensis* was caught had higher percentages of ground cover comprised of woody plants, forbs and grasses, and lower percentages of litter and bare ground. Also, capture sites had more average hits at 1 m, more-open and lower canopies, and greater average distances to nearest trees, as well as more hits on a vertical pole low (0.0–2.5 m) and fewer high (2.5–7.5 m).

Logistic regression

Overall, logistic regression of the 500 trapping stations on the five grids in 2004 resulted in the following equation:

$$\text{logit}\ (Y)=-1.055-0.013X_9+0.488X_8-0.020X_4+0.163X_{14},$$

where logit (Y) is the natural logarithm of the probability of *Sigmodon mascotensis* being present, X_9 is percent closed canopy, X_8 is average hits at 1 m, X_4 is percent litter and X_{14} is average distance to nearest tree. The probabilities for inclusion in the equation were 0.025 for the constant, <0.001 for the first three variables, and 0.002 for the fourth variable. Z-scores for the constant and four variables, respectively, were -2.243, -3.530, 5.060, -3.553, and 3.136, and standard errors (SEs) were 0.470, 0.004, 0.096, 0.006, and 0.052.

Table 4 Fisher's exact test evaluating interspecific overlap in use of space in 2004 by *Sigmodon mascotensis*, which was trapped at 125 of 500 stations, and other species captured on trap grids at Playa de Oro, Colima, Mexico, comparing number of trapping stations shared versus number expected to be shared simply by chance.

Species	Number of stations		Expected number of stations to be shared	Deviation in number of shared stations	p-value
	Where species was caught	Shared with *S. mascotensis*			
Oryzomys couesi	301 (60.2%)	102 (33.9%)	75.3	26.8	<0.001
Baiomys musculus	56 (11.2%)	27 (48.2%)	14.0	13.0	<0.001
Heteromys pictus	36 (7.2%)	2 (5.6%)	9.0	-7.0	0.004
Peromyscus perfulvus	26 (5.2%)	5 (19.2%)	6.5	-1.5	0.643
Tlacuatzin canescens	16 (3.2%)	4 (25.0%)	4.0	0.0	1.000
Reithrodontomys fulvescens	15 (3.0%)	2 (13.3%)	3.8	-1.8	0.377
Heteromys spectabilis	12 (2.4%)	1 (8.3%)	3.0	-2.0	0.310

For column indicating number of stations where species was caught, value in parentheses is percentage of the 500 trapping stations in 2004. For column indicating number of stations shared with *S. mascotensis*, value in parentheses is percentage of stations where species was caught that were shared with *S. mascotensis*.

Figure 3A shows the distribution of logit (*Y*) for capture and noncapture sites as a percentage of the total of each. McFadden's ρ^2 was 0.210, indicating the model is robust. Coefficients for two of the four variables (percent closed canopy and percent litter) were negative; sites where the species was caught tended to have lower values for these variables (Figure 3B,D). By contrast, coefficients of variable 8 (average hits at 1 m) and variable 14 (average distance to nearest tree) were positive, signifying that capture sites tended to have more vegetation hits on a 1-m vertical bar at 1-m height and were farther from trees than were noncapture sites (Figure 3C,E). Thus, stations where *S. mascotensis* was trapped tended to be more open and further from trees, as well as having more vegetation at 1 m and less litter.

Nonparametric multiplicative regression

NPMR selected eight models that had one to eight variables, respectively (for first six models, see Table 5). Progressing from models with one to three variables involved addition of a variable to the previous set (Table 5, last column). However, because models with different numbers of variables are generated independently of one another, this need not be the case, and our models with four to six variables did not simply involve addition of a variable relative to a previous set, but were new combinations including only some of those variables.

We judged the five-variable model as best overall primarily based on degree to which fit improved (ΔxR^2; Table 5). Additional variables provided relatively small increases in xR^2. The five-variable model included percent litter, average hits at 1 m, slope, maximum canopy height, and average distance to nearest tree. Given that our uniform-grid system of trapping stations produced essentially a stratified random sample of the habitat being examined, we used results from NPMR to estimate the likelihood of occurrence of *Sigmodon mascotensis* for any particular value(s) of a given variable(s) included in the model.

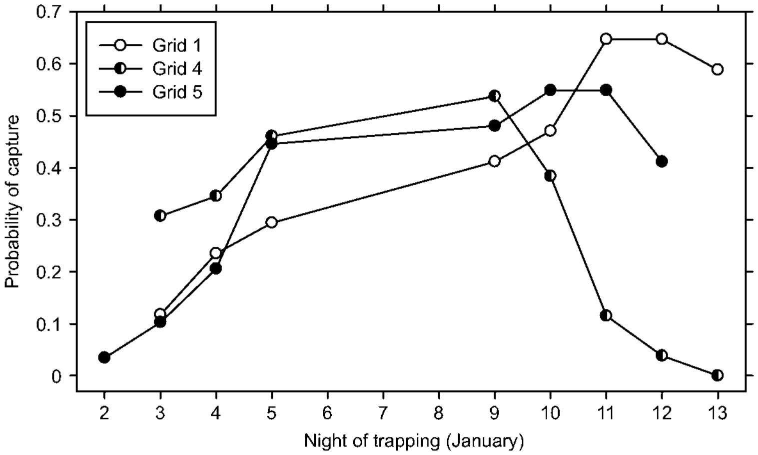

Figure 2 Probability of capture of individual *Sigmodon mascotensis* on a given night for grids 1, 4 and 5 in 2004. Estimates of probability of capture based on Model 2, where probability of capture and recapture were considered to be the same for a given night on a given grid, but could vary among nights and among grids.

For percent litter (Figure 4A), likelihood of occurrence of *Sigmodon mascotensis* was estimated to be greater than 0.3 when there was no litter. Likelihood decreased in a near-linear fashion to approximately 0.12, when litter comprised 95% of ground cover, the highest percentage found on the five grids (see Table 2).

An undulating curve of likelihood values characterized average hits at 1 m (Figure 4B), with the expectation that all stations with an average of nine to 10 hits would have *S. mascotensis* present. Data from the 500 trapping stations were insufficient to provide an estimate of likelihood for eight to nine average hits at 1 m (dotted portion of curve in

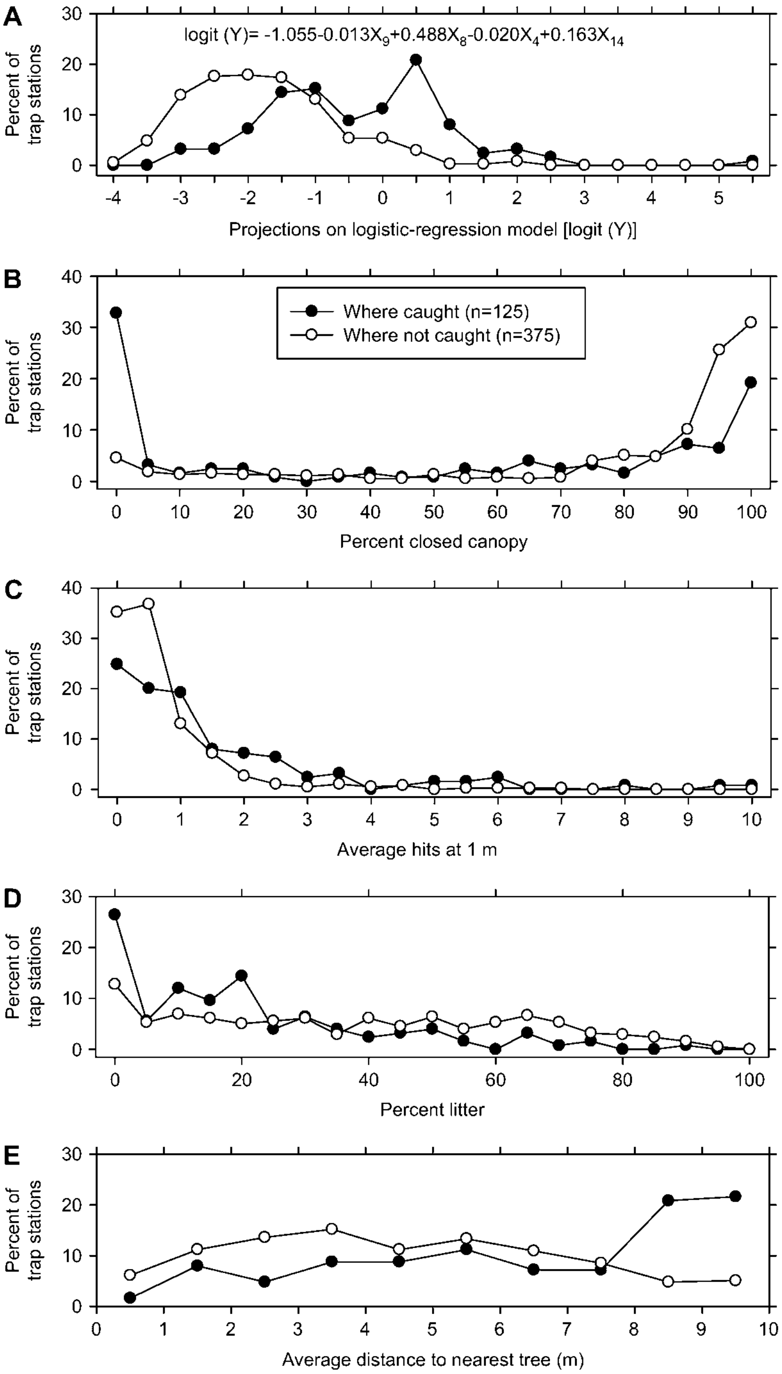

Figure 3 (A) Percentages of projections of trapping stations in given class (500 trapping stations; 125 where *Sigmodon mascotensis* was caught and 375 where it was not caught) for logistic-regression model based on vegetation-structure data from the 5 grids (2004), where logit (Y) is the natural logarithm of the probability of the species being present. Variables in equation are represented individually in the next panels: (B) percent closed canopy (X_9); (C) average hits at 1 m (X_8); (D) percent litter (X_4); and (E) average distance to nearest tree (X_{14}).

Table 5 Best NPMR models for up to six predictors used simultaneously to estimate likelihood of occurrence of *Sigmodon mascotensis* based on data from five grids at Playa de Oro, Colima, Mexico, for 2004 (500 trapping stations; 125 where *S. mascotensis* was caught and 375 where not caught). The five-variable model was judged best overall primarily based on degree of improvement in fit (i.e., ΔxR^2).

Number of variables	xR^2	ΔxR^2 from previous model	Average neighborhood size	Variables (tolerance)
1	0.1483	–	136.93	Percent canopy closed (4.99)
2	0.1980	0.0497	104.19	Average hits at 1 m (0.50) Percent canopy closed (9.98)
3	0.2292	0.0312	26.98	Average hits at 1 m (0.50) Percent closed canopy (14.98) Maximum canopy height (1.00)
4	0.2461	0.0169	29.75	Percent forbs (9.50) Average hits at 1 m (0.50) Slope (3.40) Maximum canopy height (2.00)
5	0.2560	0.0099	26.06	Percent litter (33.25) Average hits at 1 m (0.50) Slope (3.40) Maximum canopy height (2.00) Average distance to nearest tree (4.62)
6	0.2639	0.0079	25.17	Percent forbs (38.00) Percent dead wood (18.00) Average hits at 1 m (0.50) Slope (4.25) Maximum canopy height (2.00) Average distance to nearest tree (4.62)

Neighborhood size refers to sites nearby in multidimensional ‘‘environmental’’ space, the space being defined by tolerances of variables included in the model. Tolerance refers to SD of a Gaussian weighting function that controls how quickly weights diminish with distance from the target point in environmental space and, thus, determines relative influence of surrounding points in that space. Initial tolerances are functions of SDs of individual variables in the model. In local-mean models, tolerance is inversely related to importance of the variable in the model (McCune 2006).

Figure 4B). At least part of the reason for the undulating curve was that relatively few of the 500 stations had four or more average hits at 1 m (see Figure 3C of logistic-regression analysis); stations with four or more average hits at 1 m often had captures of the species. A general, broad pattern of increase in likelihood of *S. mascotensis* occurring with an increase in average hits at 1 m was identified, although we suspect that the sizeable undulations in the curve (Figure 4B) are not meaningful biologically.

The slope on the five grids varied from 0° to 17°. The likelihood of occurrence of *Sigmodon mascotensis* was approximately 0.23 for 0° to 6°, with a gradual rise to 0.33, where it stayed from 12° to 17° (Figure 4C). The maximum canopy height varied from 0 to 20 m. The likelihood of occurrence was as high as 0.53 when there was no canopy; it dropped substantially as canopy heights went from 0 to 6 m and then gradually to 17 m (Figure 4D). From 16 to 20 m in canopy height, the likelihood increased sharply to reach 0.45 at 20 m. The greatest canopy-height measurements on grids in 2004 usually were tabulated for trapping stations in proximity to planted coconut palms. Some grids were in areas that previously were part of a coconut-palm plantation but no longer received maintenance and were overgrown. The coconut palms were spaced at regular intervals and not clustered. Thus, the high canopy typically did not extend far beyond the immediate vicinity and adjacent areas often were relatively open.

Average distance to nearest tree and likelihood of occurrence of *Sigmodon mascotensis* were linearly related (Figure 4E). The likelihood estimate was 0.19 at an average distance to the nearest tree of 0.75 m and increased to 0.31 at 10.0 m.

Discussion

General demography

For January 2004, when densities of *Sigmodon mascotensis* were substantially higher than in other years of our study, slightly over half of females were reproductively active. Reproduction in *S. mascotensis* occurs throughout the year (Ceballos and Miranda 1986, 2000, Ramírez and Chávez Tovar 2005). Pregnant, receptive or lactating females have been recorded in January, March, May, July and August (Davis and Russell 1953, Matson and Baker 1986, Álvarez et al. 1987, Juárez Gómez 1992), and juveniles in January, February, May and July (Allen 1897, Ramírez-Pulido et al. 1977, Álvarez et al. 1987). For September through December, reproductive activity has not been reported for females, but males with scrotal testes have been captured in December (Juárez Gómez 1992), as well as February, April, May and July (Álvarez et al. 1987, Juárez Gómez 1992, Sánchez Hernández and Romero Almaraz 1995). No long-term study has been conducted to analyze reproductive peaks through the year.

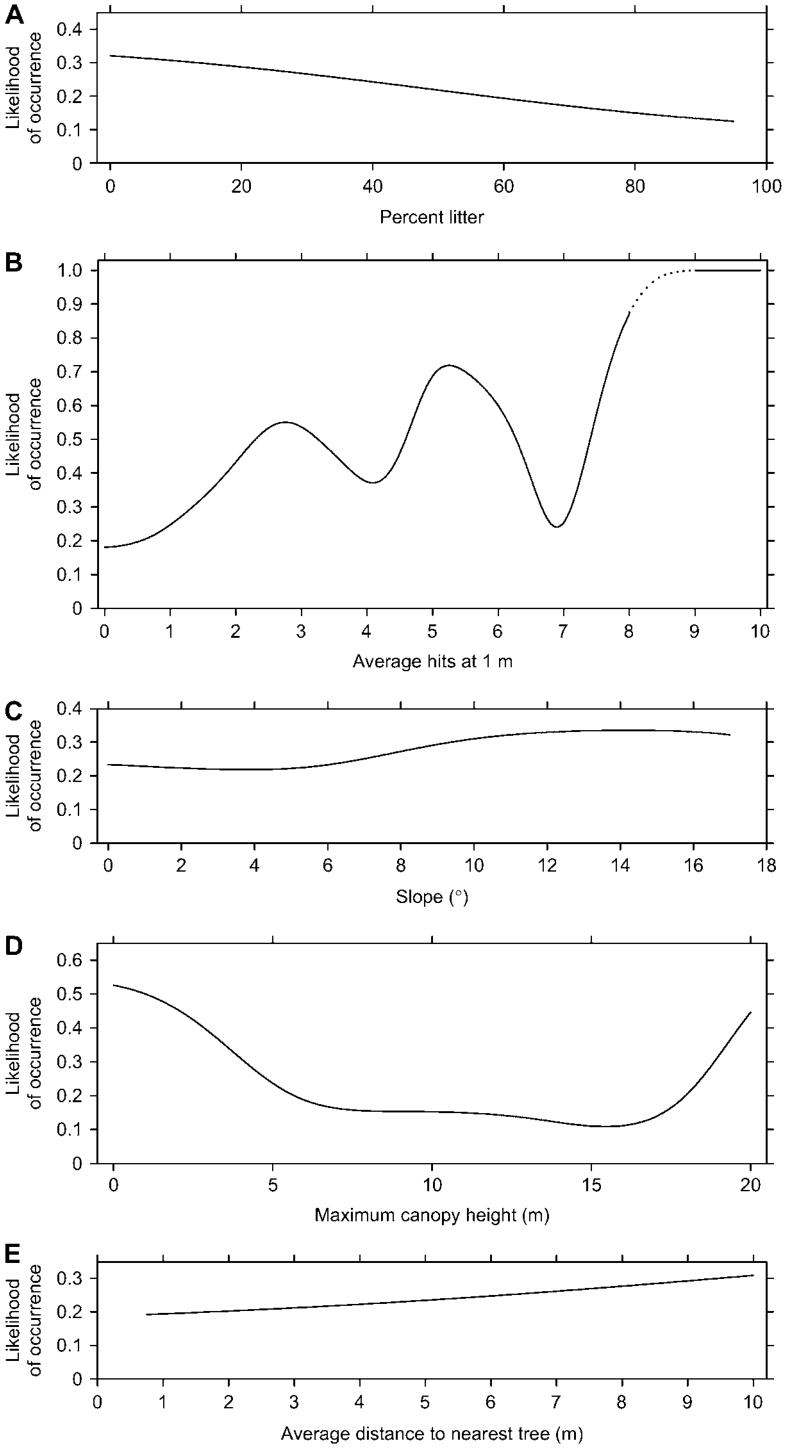

Figure 4 Likelihood of occurrence of *Sigmodon mascotensis* relative to (A) percent litter, (B) average hits at 1 m, (C) slope, (D) maximum canopy height, and (E) average distance to nearest tree for five-variable NPMR model, which was judged to be the best. Based on data from five grids at Playa de Oro, Colima, for year 2004 (500 trapping stations; 125 where *S. mascotensis* was caught and 375 where it was not caught). Dotted portion of graph in panel B indicates region where data were insufficient to make a reliable estimate.

We captured more males than females, but sex ratio did not deviate significantly from 1:1. Barrera (1952) reported 32 males and 45 females from a coconut-palm plantation in the central coast of Guerrero, results also not significantly different from a 1:1 ratio (goodness-of-fit test; G=2.21, df=1, p=0.138).

Males were heavier than females in our study. The range in mass we obtained for all adults (43.9–168.0 g) is similar at the high end to previous reports but includes smaller animals than reported elsewhere. Mass (sexes not separated) for the species was reported as 49–135 g (Ramírez and Chávez Tovar 2005). Mass of specimens from Chamela was 70–270 g (Miranda 2002a) and for northwestern coastal Guerrero 60–125.4 g (Ramírez-Pulido et al. 1977), whereas for southwestern Guerrero, the average was 110 g (Juárez Gómez 1992).

Separated by sex, the largest animals captured in our investigation, both male and female, were larger than those reported for Michoacan and Morelos. For coastal Michoacan, the mass of adult females was 62.5–124.6 g, including a pregnant female (Álvarez et al. 1987), and for adult males was 59.5–134.5 g. For Morelos, one female weighed 64 g and the average for four males was 86 g (Sánchez Hernández and Romero Almaraz 1995). For Chamela, the average mass was 116 g for males and 92 g for females (Miranda 2002a). Variation in mass of *Sigmodon mascotensis* could be owing to age and external factors given that the maximum mass for cotton rats can be highly affected by location, population density and weather (Goertz 1965). Our results suggest that there is sexual size dimorphism in *S. mascotensis*, with males being significantly heavier than females, even with pregnant females included.

Cotton rats often move in well-defined runways in vegetation, are highly mobile and can move a considerable distance in a short time (Baker 1969, Fleharty and Mares 1973). Movements by individual *Sigmodon mascotensis* have been reported for Chamela, with Collett et al. (1975) noting one individual that traveled an average of 18.1 m from capture to capture. Miranda (2002b) reported movements between consecutive captures ranged from 12 to 25 m, with maximum distances being 36–72 m. Our overall average distance between successive captures of 15.85 m (each of 160 occurrences weighted equally) is similar to measures by Collett et al. (1975) and Miranda (2002b), with variation among observations being similar to that reported by Collett et al. (1975).

The population density of *Sigmodon mascotensis* rarely has been analyzed. Barrera (1952) did not estimate population density but reported 77 individuals of *S. mascotensis* in 3 ha of sampled area, with the only other small mammal being *Rattus norvegicus* (Berkenhout 1769) (brown rat). Near Chamela, Collett et al. (1975) captured two *S. mascotensis* in a trapping grid with an effective area of 3.11 ha, and Miranda (2002b) reported 2–50/ha. Miranda (2002b) also mentioned that the highest densities of the species in tropical forest near Chamela occurred during the dry season, when there can be more than 100/ha. Our estimates of density for 2003 and 2005, years when few were caught, were 0.84–2.51/ha. For 2004, when *S. mascotensis* was abundant, the highest density we encountered was 25.31/ha, which is close to the density implied by Barrera's (1952) data.

Co-occurring species

Mammals caught on grids along with *Sigmodon mascotensis* reflect associations previously reported. In particular, the species has been reported as being associated with *Heteromys pictus* (Collett et al. 1975, Ramírez-Pulido et al. 1977, Álvarez et al. 1987, Ceballos Gonzalez 1989, Ceballos 1990, Juárez Gómez 1992, Carleton et al. 1999, Miranda 2002a). Although we captured *S. mascotensis* and *H. pictus* on the same grids, the two were captured substantially fewer times at the same sites (i.e., trapping stations) than chance would predict; the species were using habitats in different ways. Other species encountered in our study and noted in other investigations as co-occurring with *S. mascotensis* include *Baiomys musculus*, *Nyctomys sumichrasti*, *Oryzomys couesi*, *Osgoodomys banderanus*, *Peromyscus perfulvus*, *Reithrodontomys fulvescens, Xenomys nelsoni* and *Tlacuatzin canescens* (references above; also García-Estrada et al. 2002). Our data indicated that *S. mascotensis* had notable affinities for the same sites as *O. couesi* and *B. musculus*.

Several studies have reported on relative abundance of *Sigmodon mascotensis*. Barrera (1952), studying a plague of rats in a coconut-palm plantation in Costa Chica, Guerrero, reported 26.1% of captures to be *S. mascotensis*, with the rest being *Rattus norvegicus*. *Sigmodon mascotensis* represented 1.0% of animals caught at Costa Grande, Guerrero, where it was recorded only in disturbed areas such as corn fields and coconut-palm plantations, along with *Heteromys pictus* and *Reithrodontomys fulvescens* (Ramírez-Pulido et al. 1977). At Sierra de Atoyac de Álvarez in Guerrero, *S. mascotensis* was relatively rare, present only in a grassland adjacent to a pine-oak (*Pinus-Quercus*) forest (relative abundance of 0.5%; Juárez Gómez 1992). In a tropical deciduous forest in Michoacan, *S. mascotensis* comprised 7.5% of total captures (Álvarez et al. 1987), a value closest to the 9.1% of our 3-year study. García-Estrada et al. (2002) compared disturbed and undisturbed sites in a deciduous forest of Morelos; *S. mascotensis* was restricted to the disturbed site and constituted only 1.1% of mammals caught. In the Sierra de Huautla Biosphere Reserve in Morelos, *S. mascotensis* with 2.3% of total captures was less abundant than species of *Peromyscus*, *Baiomys* and *Heteromys* (Sánchez Hernández and Romero Almaraz 1995).

The proportion of small mammals captured that were *Sigmodon mascotensis* varied from year to year. A similar but less extreme pattern was noted for *Baiomys musculus* in the same grids (Schnell et al. 2008b). Paralleling interyear differences in numbers of *S. mascotensis*, total number of small mammals caught varied considerably among years; almost twice as many animals were caught in January 2004 (550 animals) than in January 2003 (286), with the number for 2005 being even lower (206). Weather records (from Chamela Biological Station, 75 km northwest along coast in Jalisco) indicate that precipitation was more than 20% greater in the year prior to our field work in January 2004 (total

12-month precipitation was 826 mm) than for 2003 (681 mm) or 2005 (652 mm). In deciduous forests, the abundance of fruits, nuts, insects and other resources exhibits strong fluctuations within and among years, which can dramatically affect abundances of small mammals (Ceballos Gonzalez 1989, Bullock and Solís-Magallanes 1990).

Schnell et al. (2008b) noted that it would be of interest to evaluate whether a competitive relationship exists between *Sigmodon mascotensis* and *Baiomys musculus,* given the suggestion by Raun and Wilks (1964) that competition occurred between *S. hispidus* and *Baiomys taylori* (Thomas 1887) (northern pygmy mouse). They reported temporal changes in densities of the two species to be inversely related, although data gathered by others (e.g., Grant et al. 1985) have not shown a similar relationship. We did find *S. mascotensis* and *B. musculus* to share specific sites more often than predicted by chance, which would provide a setting for potential competition. However, in contrast to the findings of Raun and Wilks (1964), densities of *S. mascotensis* and *B. musculus* tended to parallel one another in our study rather than be inversely related.

Probability of capture

For all three grids in 2004 where capture probability was analyzed relative to night of trapping, the probability steadily increased through the fourth night of trapping and increased for three more trapping nights on two of the grids (i.e., grids 1 and 5), whereas on the other (grid 4) it steadily decreased after trapping night 4. One factor to be considered as potentially contributing different patterns of capture probability is that there were minor differences in the temporal pattern of trapping among grids. Some grids were activated for three nights, inactive for three nights and then activated again for five nights; others were activated for four nights, inactive for three nights and activated again for four (or five) nights (Table 1). However, this potential influence can be discounted given that grids 1 and 4 had the former schedule, whereas grid 5 had the latter; a pattern among grids not congruent with that for probability of capture.

Schnell et al. (2008b) analyzed data for *Baiomys musculus* on the grids we studied during 2003–2005 plus grids set in 2006 and 2007 in northern Colima, detecting differences among nights. For coastal grids, probability of capture increased from trapping nights 1–4 and then decreased, as shown in our findings for *Sigmodon mascotensis* on grid 4; for the northern grids, capture probability of *B. musculus* increased until trapping night 6 and leveled for the last two nights. Schnell et al. (2008b) suggested for *B. musculus* that an increasing capture probability with night of trapping could result from adjustment of the species to disturbance associated with placement of traps, or it could reflect that animals had located a ready food source at the trap site. Both factors could be influencing *S. mascotensis*.

Ecological characteristics

Sigmodon mascotensis occupies a wide range of habitats, including disturbed areas (Ceballos and Miranda 1986, 2000), being recorded more commonly in grasslands by some investigators (Matson and Baker 1986). It often frequents areas near bodies of water, including an irrigation canal in dense grass with *Acacia* in central Michoacan (Zimmerman 1970), a closed tropical-deciduous vegetation along a river in coastal Michoacan (Álvarez et al. 1987), streamside agricultural areas in Zacatecas (Matson and Baker 1986), a coconut-palm plantation near a lagoon in Guerrero (Ramírez-Pulido et al. 1977) and an arroyo forest in Jalisco (Ceballos Gonzalez 1989). Our grids all were close to wetlands (Figure 1).

At some localities, *Sigmodon mascotensis* is common in agricultural and other disturbed areas (Ramírez and Chávez Tovar 2005). It has been trapped in banana and coconut-palm plantations with dense grass (Barrera 1952, Ramírez-Pulido et al. 1977); in coffee plantations and near corn fields along a tropical deciduous forest in Guerrero (Juárez Gómez 1992); in tropical deciduous forest disturbed by fire, wood extraction and grazing in Morelos (García-Estrada et al. 2002); and in grasslands and near corn fields in Jalisco (Ceballos Gonzalez 1989). Often, areas adjacent to our grids were highly disturbed and some grids were near agricultural fields.

Near Chamela in Jalisco, Ceballos Gonzalez (1989) reported *Sigmodon mascotensis* abundant in grasslands and scarce in deciduous forests. Elsewhere in Jalisco the species was observed among cattails (*Typha*), as well as in a salt marsh along the coast and on a grassy hillside with *Acacia* near the edge of a tropical deciduous forest (Zimmerman 1970) and among grasses and other understory plants in a pine forest (Hooper 1955). In Morelos, *S. mascotensis* was in a disturbed tropical-deciduous forest with thorny legume shrubs (García-Estrada et al. 2002) and in dry areas with thick grasses, herbs and shrubs (Davis and Russell 1953). In Michoacan, it was trapped in closed, low tropical-deciduous vegetation and in partially closed, low thorny vegetation (Álvarez et al. 1987) and, in Guerrero, in grassy areas next to pine-oak forest (Juárez Gómez 1992). Our analyses showed that trapping stations where *S. mascotensis* was caught tended to have higher percentages of ground cover made up of woody plants, forbs and grasses, with lower percentages of litter and bare ground. No grid in our study was primarily grassland, although we have caught the species in such areas elsewhere in Colima.

Near Chamela, Jalisco, *Sigmodon mascotensis* was captured on a mountain covered with tall trees and low dense understory formed by shrubs, bushes and grasses (Collett et al. 1975). Trapping stations where we captured *S. mascotensis* tended to have an open canopy. In Colima, it has been trapped in brush piles of palm fronds and other litter in a palm plantation (Hooper 1955). In our logistic-regression and NPMR analyses, litter appeared to have a negative effect on occurrence of *S. mascotensis*. The species also occurs in rocky areas (Hooper 1955, García-Estrada et al. 2002), and Sánchez Hernández and Romero Almaraz (1995) noted that, although *S. mascotensis* preferred dense understory, the most important feature for its shelter was rocky ground. We did not find rocks to be important relative to occurrence of *S. mascotensis*; however, rocky areas constituted only small percentages of our grids.

Comparison of results of logistic regression and nonparametric multiplicative regression

Our logistic-regression equation included four habitat variables, whereas five were included in the NPMR solution we deemed best. Percent litter and average distance to nearest tree were in both solutions, and both variables showed a linear relationship with likelihood of occurrence of *Sigmodon mascotensis*. Average hits at 1 m also was in both solutions; although NMPR identified an undulating pattern for this variable with likelihood of occurrence (Figure 4B), the likelihood increased notably from where there were no or few hits to where the number of hits was at the maximum we recorded in this study. The percent closed canopy was the other variable included in the logistic-regression solution and, whereas it was not in the NMPR model we judged best, it was included in the best NMPR models developed that included only one or two variables. Slope, which was included in the NMPR solution we selected, never was under consideration for selection during the stepwise procedure used to develop a logistic-regression equation. Maximum canopy height was not included in the logistic-regression equation but was in the NMPR model; this variable had a notably nonlinear association with likelihood of occurrence (Figure 4D) and, thus, was not a good candidate for inclusion in the logistic-regression equation. NMPR is able to accommodate patterns in variables that are highly nonlinear, whereas logistic regression is not likely to select such variables (unless they have been appropriately transformed to a more or less linear or step pattern before the analysis). Logistic regression and NMPR assess associations of habitat variables and with presence/absence in notably different ways, and both have been useful in evaluating habitat preferences of *Sigmodon mascotensis*.

Comparison with closely related species of *Sigmodon*

Most taxonomic analyses suggest *Sigmodon mascotensis* and *Sigmodon arizonae* (Mearns 1890) (Arizona cotton rat) are sister clades (e.g., Carroll et al. 2005), and that *Sigmodon hispidus* is sister to this group (Carroll and Bradley 2005). *Sigmodon arizonae* is not well-known ecologically. It most consistently has been trapped in open grassy and herbaceous settings, usually in the presence of ample water (Carleton et al. 1999). *Sigmodon hispidus* is the species with widest distribution and is the best studied *Sigmodon*. In Mexico, distribution of *S. hispidus* is somewhat complementary to that of *S. mascotensis*.

No difference in movement of male and female *Sigmodon mascotensis* in January in Colima was noted during our investigation. Studies of *S. hispidus* have suggested that males move farther than females and home ranges of males are larger (Erickson 1949, Stickel and Stickel 1949, Fleharty and Mares 1973, Cameron and Spencer 1985). Also, we detected no evidence of a deviation from a 1:1 sex ratio in *S. mascotensis*. The sex ratio (male:female) for *S. hispidus* was 1:0.95 in Texas (Stickel and Stickel 1949) and 1:0.81 in Georgia (Erickson 1949), not substantially different from 1:1. Goertz (1965) noted that the sex ratio in S. *hispidus* can deviate significantly from 1:1 after a cold winter.

Densities of *Sigmodon hispidus* are as variable as those of *S. mascotensis* but show strong bimodal population fluctuations (Cameron and Spencer 1981). In Texas, densities were 0.5–29.65/ha (Stickel and Stickel 1949, Cameron 1977), in Georgia 4.7–69/ha (Erickson 1949, Odum 1955), in Florida 10–25/ha (Layne 1974), in Kansas 0.2–20/ha (Fleharty et al. 1972), and in Durango, Mexico, 25–51/ha (Petersen 1973).

Sigmodon hispidus, as with most cotton rats, frequents grassy environments (Odum 1955, Fleharty and Mares 1973, Kaufman and Fleharty 1974) and occurs in prairies (Stickel and Stickel 1949, Fleharty and Mares 1973, Smith and Vrieze 1979), deserts (Matson and Baker 1986) and cultivated areas (McClenaghan and Gaines 1978). In Zacatecas and Oklahoma, *S. hispidus* occurred mainly in grassy open areas (Matson and Baker 1986, Stancampiano and Schnell 2004). In Texas, it was reported at sites with dense cover (Stickel and Stickel 1949). *Sigmodon hispidus* selected dense undergrowth and a protective overstory in west-central Kansas (Fleharty and Mares 1973) and dense stands of grasses intermixed with forbs in north-central Kansas (Kaufman and Fleharty 1974). Our data suggest that *S. mascotensis* occurs more frequently in woodlands (albeit open ones) than probably would be the case for *S. hispidus*.

Acknowledgements

We thank E. Meneses for help in many ways to facilitate our studies of mammals in Colima. Numerous students and some other faculty members from Mexico and the United States provided significant assistance with our work on the trapping grids. L.A. Lara Ortiz and A. Morales Ortiz helped build the database and C.J. Poindexter assisted with some statistical analyses. The late L.A. Pérez Jiménez identified plants collected in the study area. Three anonymous reviewers provided thoughtful and helpful comments on earlier versions of the manuscript. The Consejo Nacional de Ciencia y Tecnología (CONACYT) supported various aspects of this project (Grant 102338). Appropriate permits were obtained from the Instituto Nacional de Ecología, Dirección General de Vida Silvestre FAUT.0103 to C. Sánchez-Hernández, and research protocols were approved by the Animal Care and Use Committee of the University of Oklahoma.

References

Allen, J.A. 1897. Further notes on mammals collected in Mexico by Dr. Audley C. Buller, with descriptions of new species. Bull. Am. Mus. Nat. Hist. 9: 47–58.

Álvarez, T., J. Arroyo-Cabrales and M. González Escamilla. 1987. Mamíferos (excepto Chiroptera) de la costa de Michoacán, México. An. Esc. Nac. Cienc. Biol. Mex. 31: 13–62.

Baker, R.H. 1969. Cotton rats of the *Sigmodon fulviventer* group. Misc. Publ. Mus. Nat. Hist. Univ. Kans. 51: 177–232.

Baker, R.H. and J.K. Greer. 1962. Mammals of the Mexican state of Durango. Publ. Mus. Mich. State Univ. Biol. Ser. 2: 25–154.

Barrera, A. 1952. Algunas observaciones de las ratas que constituyen plaga en los cocotales de la Costa Chica de Guerrero. Fitófilo 6: 5–10.

Berryman, S. and B. McCune. 2006. Estimating epiphytic macrolichen biomass from topography, stand structured and lichen community data. J. Veg. Sci. 17: 157–170.

Bullock, S.H. and A. Solís-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22: 22–35.

Cameron, G.N. 1977. Experimental species removal: demographic responses by *Sigmodon hispidus* and *Reithrodontomys fulvescens*. J. Mammal. 55: 488–506.

Cameron, G.N. and S.R. Spencer. 1981. *Sigmodon hispidus*. Mamm. Species 158: 1–9.

Cameron, G.N. and S.R. Spencer. 1985. Assessment of space-use patterns in the hispid cotton rat (*Sigmodon hispidus*). Oecologia (Berl.) 68: 133–139.

Carleton, M.D., R.D. Fisher and A.L. Gardner. 1999. Identification and distribution of cotton rats, genus *Sigmodon* (Muridae: Sigmodontinae) of Nayarit, Mexico. Proc. Biol. Soc. Wash. 112: 813–856.

Carroll, D.S. and R.D. Bradley. 2005. Systematics of the genus *Sigmodon*: DNA sequences from beta-fibrinogen and cytochrome *b*. Southwest. Nat. 50: 342–349.

Carroll, D.S., L.L. Peppers and R. Bradley. 2005. Molecular systematics and phylogeography of the *Sigmodon hispidus* species group. In: (V. Sánchez-Cordero and R.A. Medellín, eds.) Contribuciones mastozoológicas en homenaje a Bernado Villa. Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México and CONABIO, México, D.F. Mexico. pp. 87–100.

Ceballos, G. 1990. Comparative natural history of small mammals from tropical forests in western Mexico. J. Mammal. 71: 263–266.

Ceballos, G. and A. Miranda. 1986. Los mamíferos de Chamela, Jalisco: manual de campo. Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., Mexico. pp. 436.

Ceballos, G. and A. Miranda. 2000. Guía de campo de los mamíferos de la costa de Jalisco, México. Fundación Ecológica de Cuixmala A.C., Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México, D.F., Mexico. pp. 502.

Ceballos Gonzalez, G.J. 1989. Population and community ecology of small mammals from tropical deciduous and arroyo forests in western Mexico. PhD dissertation, University of Arizona, Tucson, AZ, USA.

Collett, S.F., C. Sánchez Hernández, K.A. Shum Jr., W.R. Teska and R.H. Baker. 1975. Algunas características poblacionales demográficas de pequeños mamíferos en dos hábitats mexicanos. An. Inst. Biol. Univ. Nac. Auton. Mex. Ser. Zool. 46: 101–123.

Davis, W.B. and R.J. Russell. 1953. Aves y mamíferos del estado de Morelos. Rev. Soc. Mex. Hist. Nat. 14: 77–121.

Erickson, A.B. 1949. Summer populations and movements of the cotton rat and other rodents on the Savannah River Refuge. J. Mammal. 30: 133–140.

Fleharty, E.D. and M.A. Mares. 1973. Habitat preference and spatial relations of *Sigmodon hispidus* on a remnant prairie in west-central Kansas. Southwest. Nat. 18: 21–29.

Fleharty, E.D., J.R. Choate and M.A. Mares. 1972. Fluctuations in population density of the hispid cotton rat: factors influencing a ‘‘crash’’. Bull. S. Calif. Acad. Sci. 71: 132–138.

García-Estrada, C., M.L. Romero-Almaraz and C. Sánchez-Hernández. 2002. Comparison of rodent communities in sites with different degrees of disturbance in deciduous forest of southeastern Morelos, Mexico. Acta Zool. Mex. Nueva Ser. 85: 153–168.

Goertz, J.W. 1965. Sex, age and weight variation in cotton rats. J. Mammal. 46: 471–477.

Grant, W.E., P.E. Carothers and L.A. Gidley. 1985. Small mammal community structure in the postoak savanna of east-central Texas. J. Mammal. 66: 589–594.

Hayne, D.W. 1949. Calculation of size of home range. J. Mammal. 30: 1–18.

Hooper, E.T. 1955. Notes on mammals on western Mexico. Occas. Pap. Mus. Zool. Univ. Mich. 565: 1–26.

Instituto Nacional de Estadística, Geografía e Informática. 2006. Anuario estadístico del estado de Colima. 2006 ed. Instituto Nacional de Estadística, Geografía e Informática, Aguascalientes, Aguascalientes, Mexico.

Juárez Gómez, J.R. 1992. Distribución altitudinal de los roedores de la Sierra de Atoyac de Álvarez, Guerrero. Bachelor's thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F., Mexico.

Kaufman, D.W. and E.D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwest. Nat. 18: 443–452.

Layne, J.N. 1974. Ecology of small mammals in flatwoods habitat in north-central Florida, with emphasis on the cotton rat (*Sigmodon hispidus*). Am. Mus. Novit. 2544: 1–48.

Matson, J.O. and R.H. Baker. 1986. Mammals of Zacatecas. Spec. Publ. The Museum, Texas Tech Univ. 24: 1–88.

McClenaghan, L.R. Jr. and M.S. Gaines. 1978. Reproduction in marginal populations of the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. Occas. Pap. Mus. Nat. Hist. Univ. Kans. 74: 1–16.

McCune, B. 2006. Nonparametric multiplicative regression for habitat modeling. http://www.pcord.com/NPMRintro.pdf.

McCune, B. and M.J. Mefford. 2004. HyperNiche. Multiplicative habitat modeling. Version 1.0. MjM Software, Gleneden Beach, Oregon, USA. pp. 24.

Miranda, A. 2002a. Deforestación y fragmentación del hábitat: consecuencias ecológicas sobre la fauna de mamíferos de la selva tropical estacional en el occidente de México. PhD dissertation, Instituto de Ecología, Universidad Nacional Autónoma de México, México, D.F., Mexico.

Miranda, A. 2002b. *Sigmodon mascotensis*. In: (F.A. Noguera, J.H. Vega Rivera, A.N. García Aldrete and M. Quesada Avendaño, eds.) Historia natural de Chamela. Instituto de Biología, Universidad Nacional Autónoma de México. México, D.F., Mexico. pp. 437–438.

Musser, G.G. and M.D. Carleton. 2005. Superfamily Muroidea. In: (D.E. Wilson and D.M. Reeder, eds.) Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Vol. 2. Johns Hopkins University Press, Baltimore, MD, USA. pp. 894–1532.

Odum, E.P. 1955. An eleven year history of a *Sigmodon* population. J. Mammal. 36: 368–378.

Otis, D.L., K.P. Burnham, G.C. White and D.R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62: 1–135.

Petersen, M.K. 1973. Interactions between the cotton rats, *Sigmodon fulviventer* and *S. hispidus*. Am. Midl. Nat. 90: 319–333.

Ramírez, J. and J. Chávez Tovar. 2005. *Sigmodon mascotensis*. In: (G. Ceballos and G. Oliva, coordinators) Los mamíferos silvestres de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and Fondo de Cultura Económica, México, D.F., Mexico. pp. 803–804.

Ramírez-Pulido, J., A. Martínez and G. Urbano. 1977. Mamíferos de la Costa Grande de Guerrero, México. An. Inst. Biol. Univ. Nac. Auton. Mex. Ser. Zool. 48: 243–292.

Raun, G.G. and B.J. Wilks. 1964. Natural history of *Baiomys taylori* in southern Texas and competition with *Sigmodon hispidus* in a mixed population. Tex. J. Sci. 16: 28–49.

Rohlf, F.J. and D.E. Slice. 1999. BIOMstat for Windows. Exeter Software, Setauket, New York, USA. pp. 58.

Sánchez Hernández, C. and M.L. Romero Almaraz. 1995. Mastofauna silvestre del área de reserva Sierra de Huautla (con énfasis en la región noreste). Universidad Autónoma del Estado de Morelos and FOMES, Secretaría de Educación Pública, Cuernavaca, Morelos, Mexico. pp. 146.

Schnell, G.D., M.L. Kennedy, C. Sánchez Hernández, M.L. Romero-Almaraz, B.D.N. Estevez, J. Guerrero, T.L. Best, M.C. Wooten and R.D. Owen. 2008a. Habitat preference of the endemic tawny deermouse (*Peromyscus perfulvus*), a species of conservation concern. Southwest. Nat. 53: 9–20.

Schnell, G.D., C.J. Poindexter, C. Sánchez Hernández, M.L. Romero-Almaraz, M.L. Kennedy, T.L. Best, M.C. Wooten and A.P. Jiménez. 2008b. Demographic features and habitat preferences of southern pygmy mice (*Baiomys musculus*) in Colima, Mexico. Can. J. Zool. 86: 507–524.

Slade, N.A. and R.K. Swihart. 1983. Home range indices for the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. J. Mammal. 64: 580–590.

Smith, A.J. and J.M. Vrieze. 1979. Population structure of everglade rodents: responses to a patchy environment. J. Mammal. 60: 778–794.

Stancampiano, A. and G.D. Schnell. 2004. Microhabitat affinities of small mammals in southwestern Oklahoma. J. Mammal. 85: 940–947.

Stickel, L.F. and W.H. Stickel. 1949. A *Sigmodon* and *Baiomys* population in ungrazed and unburned Texas prairie. J. Mammal. 30: 141–150.

Systat Software. 2007. Systat 12: statistics III. Systat Software, Inc. San Jose, CA, USA. pp. 471.

White, G.C. 2007. Program MARK: mark and recapture survival rate estimation. Version 4.3, 25 June 2007. http://www.cnr.colostate.edu/~gwhite/mark/m.

White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement): 120–138.

Zimmerman, E.G. 1970. Karyology, systematics and chromosomal evolution in the rodent genus *Sigmodon*. Publ. Mus. Mich. State Univ. Biol. Ser. 4: 385–454.