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## ORIGINAL INVESTIGATION

### Microhabitat preferences and spatial distribution of the vesper rat (*Nyctomys sumichrasti*) in Colima, Mexico

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#### Abstract

The vesper rat (*Nyctomys sumichrasti*), a little-known arboreal rodent, was encountered during mark-recapture studies in Colima, Mexico, in January 2003–2007. We trapped on the Pacific coast at Playa de Oro (2003–2005) and in northern Colima (2006–2007). Each year five trap grids were established in heavily vegetated areas and typically run for 8 nights (100 trap stations per grid, each station with a ground trap and an arboreal trap elevated 1–2 m, 10 × 10 configuration with adjacent stations 10 m apart; 1,600 trap-nights per grid; 40,000 trap-nights total). *Nyctomys sumichrasti* occurs throughout most of Colima. On grids we captured 29 individuals a total of 41 times, with 90.2% of captures in arboreal traps and 69.0% of animals being adults. The sex ratio of adults was 1.22:1 (males:females), not statistically different from 1:1. Most adult females (77.8%) were pregnant or lactating. Mean mass was 41.3 and 38.6 g for males and females, respectively ( $P > 0.05$ ). Mean greatest distances traveled were longer for males (60.6 m) than females (20.2 m), with an overall mean of 40.4 m. One to six individuals were captured on 9 of 25 grids, with density estimates of 0.87–4.09/ha. We contrasted 14 environmental measures (most involving vegetation structure) for stations where *N. sumichrasti* was caught and not caught using logistic regression and nonparametric multiplicative regression, finding the species frequented sites flat to moderate in slope with considerable ground litter and relatively sparse high vegetation. In northern Colima, *N. sumichrasti* used areas with close trees, an open understory, and little grass. Other studies indicate the species sometimes occupies similar areas but with a relatively dense understory.

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#### Introduction

The vesper rat (*Nyctomys sumichrasti*), a stocky, medium-sized rodent with a large head, short face,

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distinctive tawny-brown to orange coloring on upperparts, and cream-colored underparts (Hunt et al., 2004), is found along the Pacific and Gulf coasts of Mexico from southern Jalisco and Veracruz to central Panama, excluding the Yucatán Peninsula (Musser and Carleton, 2005). It has been found from lowlands to 1,800 m in evergreen and semideciduous forest, as well as tall second growth (Reid, 2009). In general, there is a dearth of current information on the species (Hunt et al., 2004). Some information on general ecology of *N. sumichrasti* was included in reports of general surveys of small mammals by Fleming (1970) in Panama, Ceballos (1990) in Jalisco, and Sánchez-Hernández et al. (1999) in Michoacán.

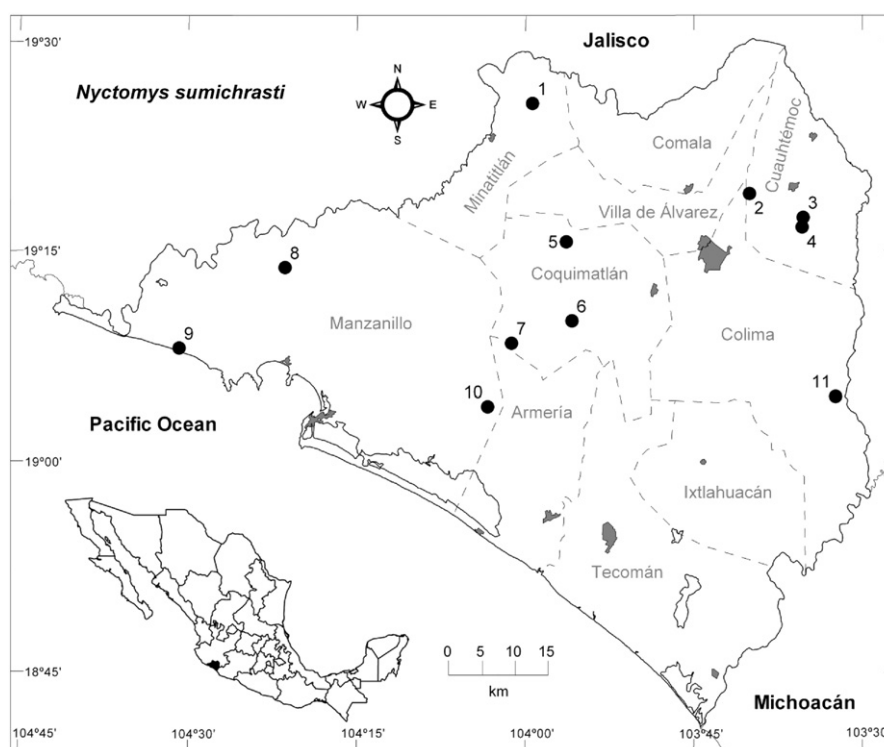
Habitat use has not been described in detail, and there are few reports on general demography or population size. The species is present in areas designated as biodiversity hotspots (Hamblen, 2004; Shi et al., 2005), including tropical dry forests, that potentially are at risk and in need of further study (Sánchez-Azofeifa et al., 2005). Our purposes were to investigate the status and ecology of *N. sumichrasti* in Colima, Mexico, obtaining population-density estimates at several localities and evaluating quantitative habitat data. In addition, we report selected demographic data, including sex ratio, age, and reproductive status.

## Material and methods

### Study areas and trapping

Each January 2003–2007 we established five 1-ha trapping grids (25 grids total) at localities in the state of Colima, Mexico. January is part of the dry season in this region; typically, days are warm and nights cool (Instituto Nacional de Estadística, Geografía e Informática, 1999), with little day-to-day variation in temperature. For 2003–2005, our study site was at Playa de Oro (Fig. 1, locality 9), while in 2006–2007 grids were in northern Colima at Rancho La Angostura (locality 2 in 2006) and sites close to Miguel de la Madrid Airport (locality 4 in 2006 and localities 3 and 4 in 2007).

Each grid had 100 trap stations (10 × 10 configuration), with adjacent stations 10 m apart. Two Sherman live traps (7.5 × 9.0 × 23.0 cm; H. B. Sherman Traps, Tallahassee, Florida) were placed at each station: one ground trap and one arboreal trap 1–2 m above ground on a thin plywood platform (12.5 × 34.5 cm) attached to the vegetation. Traps were set and baited with rolled oats each day and checked each morning starting at sunrise. None of the 25 grids overlapped spatially. Those at Playa de Oro were within 1 km of the ocean at elevations < 10 m asl. Grids were mostly in tropical dry



**Fig. 1.** Locations in state of Colima where *Nyctomys sumichrasti* has been captured. Inset map indicates location of Colima in Mexico. Some numbered symbols represent two geographically close localities (see gazetteer in Appendix). Grids in coastal Colima for 2003–2005 were at locality 9. Those in northern Colima for 2006 were at localities 2 and 4, while for 2007 they were at localities 3 and 4. Water bodies are shown (outlined), as are some cities and towns (shaded). Dashed lines indicate boundaries of 10 municipalities in the state that are named after the principal city or town in each.

deciduous forest, with some elements of thorn forest and mangrove (Table 1). Schnell et al. (2008a, b) provided further descriptions of the coastal grids. Elevations of grids in northern Colima were 700–765 m asl. Grids at Rancho La Angostura (Fig. 1, locality 2) were in tropical moist forest within an overall landscape fragmented due to cultivated agriculture and livestock (Schnell et al., 2008b); these grids were adjacent to a water course where some gallery forest persisted. Sites of the other northern grids (Fig. 1, localities 3 and 4) were fragmented and used for agriculture in the past. However, there had been restricted human entry to these areas for >30 years prior to our studies and,

consequently, sites were relatively undisturbed and characterized as moist forest intermixed with grass-dominated areas (for details, see Schnell et al., 2008b).

For each capture, we recorded sex, age, reproductive status (based on external condition of reproductive organs), body mass, and grid capture station. Females were categorized as adults if pregnant, receptive, lactating, or postlactating (or inactive but with adult color and size); males with scrotal testes were considered adults. Adults typically had more reddish upperparts, usually weighting >37 g. Subadults were similar in color but more brownish and usually <37 g. Juveniles tended to be dusky gray and <30 g. Animals were

**Table 1.** General description of each grid in Colima, Mexico, with sampling dates in January (modified from Schnell et al. 2008b).

Grid number (January dates)	Description
<b>2003 (coastal Colima)</b>	
1 (2-5, 9-12)	Thorn forest with some palm trees in proximity to mangroves
2 (2-5, 9-12)	Thorn forest with some palm trees in proximity to mangroves
3 (3-5, 9-13)	Thorn forest adjacent to palm plantation
4 (3-5, 9-13)	Thorn forest adjacent to palm plantation
5 (3-5, 9-13)	Mixture of grassy patches and palm trees associated with undergrowth of thorn forest
<b>2004 (coastal Colima)</b>	
1 (3-5, 9-13)	Mixture of thorn forest and mangrove, with some palms
2 (2-5, 9-12)	Mixture of thorn forest and mangrove, with some palms
3 (2-5, 9-12)	Thorn forest in proximity to palm plantation
4 (3-5, 9-13)	Mixture of grassy patches, palm trees, and thorn forest adjacent to agricultural fields
5 (2-5, 9-13)	Mixture of grassy patches, palm trees, and thorn forest adjacent to agricultural fields
<b>2005 (coastal Colima)</b>	
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 patches, and xerophilous scrubs
4 (2-6, 10-12)	Mixture of grassy patches, palm trees associated with dense undergrowth of thorn forest, and patches of mangrove
5 (3-6, 10-13)	Mixture of grassy patches, palm trees, and thorn forest
<b>2006 (northern Colima)</b>	
1 (2-6, 10-12)	Tropical deciduous forest with tall, mature trees and dense understory, bordered by small stream
2 (2-6, 10-12)	Tropical deciduous forest with tall, mature trees and dense understory, bordered by small stream
3 (3-6, 10-13)	Thorn forest with sparse understory vegetation intermixed with patches of tall grass (height ca. 1.0–1.5 m)
4 (3-6, 10-13)	Thorn forest with patches of tall grass associated with small stream and riparian habitat of dense vines and large deciduous trees
5 (3-6, 10-13)	Thorn forest with sparse understory vegetation intermixed with patches of tall grass (height ca. 1.0–1.5 m)
<b>2007 (northern Colima)</b>	
1 (2-6, 10-12)	Tropical deciduous forest with some mature trees, thin/sparse understory with some young thorn trees. Included partially cleared, unimproved road traversing grid
2 (2-6, 10-12)	Mixture of tropical deciduous with large, mature trees and thorn-forest elements
3 (2-6, 10-12)	Dense thorn forest with vines creating low, thick canopy cover. Some areas with mature deciduous trees and others with patches of tall grass in open areas
4 (3-6, 10-13)	Dense thorn forest with vines creating low, thick canopy cover. Some areas with mature deciduous trees and others with patches of tall grass in open areas
5 (3-6, 10-13)	Tall dense grasses (1.0–3.0 m) with isolated trees

For 2003–2005, all grids at locality 9 (Fig. 1). For 2006, grids 1–2 at locality 2 and grids 3–5 at locality 4. In 2007, grids 1–4 at locality 3 and grid 5 at locality 4.

tagged in both ears using uniquely numbered Monel No. 1 ear tags (National Band and Tag Company, Newport, Kentucky) and released at the station of capture.

### Structure of vegetation

Vegetation structure was evaluated based on 14 variables following techniques used by Schnell et al. (2008a, b). For 2004–2007, variables were measured at points about 1 m from each trap station (2000 points total). Using a 1-m square, we estimated ground cover to the nearest 5% for seven cover types (first seven variables in Table 2). Number of shrub or grass stems hitting a 1-m bar at 1-m height was determined four times (once in each cardinal direction from a central point) and the average calculated (variable 8). Canopy cover (percent closed, variable 9) was obtained using a spherical densitometer (model C, Forest Densitometers, Bartlesville, Oklahoma) and slope (variable 10) with a clinometer. With a 7.5-m vertical pole marked at each decimeter, we determined the number of decimeter intervals within which vegetation touched the pole, with results summed for 0–2.5 m (maximum of 25 hits; variable 11) and 2.5–7.5 m (maximum of 50 hits; variable 12). Maximum height of canopy was recorded to the nearest 0.5 m (variable 13). Distance to nearest tree ( $\geq 10$  cm dbh [diameter at breast height]) was determined for each of four quadrants (edges being the cardinal directions) and the average taken (variable 14); distances  $\geq 10$  m were entered as 10 m.

In 2003, similar measures were taken, but only at 25 points/grid equally spaced among trap sites. Using resulting values for each variable, we estimated the variable for each trap station using ordinary and point kriging in the program Surfer 8 (Golden Software, Inc., 2002). These estimates were then treated the same as those for trap stations for other years.

Correlations ( $r$ ) between variable pairs over the 2,500 trap stations studied ranged from 0.000 to 0.577, but generally were low, with an average absolute correlation of 0.180; the average  $R^2$ -value between pairs of variables was only 0.053. Thus, there was relatively little redundancy among variables.

### Logistic regression and nonparametric multiplicative regression

Using stepwise logistic regression (Systat Software Inc., 2007), we evaluated the relationship between vegetation structure at trap stations where *N. sumichrasti* was caught and not caught. The dependent variable was presence or absence (1 or 0) of *N. sumichrasti*, with the 14 environmental measures used as potential independent variables. The significance to include or remove a variable was set at 0.05, with maximum number of steps

set at 10. McFadden's  $\rho^2$  statistic, which can vary from 0 to 1, was used to evaluate resulting models as a whole, with higher values indicating more significant results (Systat Software Inc., 2007).

Nonparametric multiplicative regression (NPMR) as implemented in the program HyperNiche (version 1.32; McCune and Mefford, 2004) also was employed to model habitat use based on the 14 environmental variables recorded at trap stations. NPMR creates habitat models, combining predictor variables multiplicatively rather than additively. The overall form of the response surface need not be specified in advance (e.g., response of a species to given environmental variable could be linear, but responses in form of normal or bimodal distributions also could be identified). NPMR does not produce an equation but optimizes data fit without reference to a specific global model. Results are represented as response curves and surfaces.

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 a kernel function. We employed the local-mean (LM) model type in HyperNiche, where weighting around each target point was based on a Gaussian (hump-backed) function. An exhaustive search was made for the best model, where combinations of variables and tolerances (i.e., the SDs used in the Gaussian smoothers) were evaluated. Starting with a single variable, others are added until no improvement in fit is achieved. We used  $\log_{10} B$  as a measure of model fit, which is the null deviance minus the residual deviance (i.e., deviance of a model with no predictors), with the result divided by 4.60517 (McCune, 2006). The measure can be negative because each data point is excluded when estimating response at that point. After an 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  $\log B$ , then selecting the best overall model for predicting likelihood of occurrence of *N. sumichrasti*.

### Other statistical tests and density estimation

Univariate statistical tests, including one- and two-way ANOVAs, were conducted with BIOMstat for Windows 3.3q (Rohlf and Slice, 1999). Initially, we used program MARK (White, 2007) to estimate abundance of *N. sumichrasti*. However, while the program provided useful estimates of capture probability, robust abundance estimates were not achieved for most grids due to the numbers of animals encountered and distributions of captures and recaptures. Therefore, abundance was estimated based on minimum number of males and females known to be alive when sampling occurred (Krebs, 1966; Slade and Blair, 2000). To obtain densities

**Table 2.** Mean  $\pm$  SD (range) of 14 variables providing assessment of habitat at stations of five trap grids per year (2003–2007) where *Nyctomys sumichrasti* was captured and not captured.

Variable	2003–2005 (coastal Colima)		2006–2007 (northern Colima)		2003–2007 (all Colima grids)	
	Captured (n = 18)	Not captured (n = 1482)	Captured (n = 18)	Not captured (n = 982)	Captured (n = 36)	Not captured (n = 2464)
1 Woody plants (%)	5.8 $\pm$ 13.57 (0–58)	6.2 $\pm$ 9.72 (0–95)	8.6 $\pm$ 8.71 (0–25)	5.8 $\pm$ 9.82 (0–75)	7.2 $\pm$ 11.33 (0–58)	6.0 $\pm$ 9.76 (0–95)
2 Forbs (%)	5.9 $\pm$ 7.87 (0–28)	9.8 $\pm$ 17.08 (0–95)	7.2 $\pm$ 3.08 (5–15)	7.6 $\pm$ 11.35 (0–100)	6.6 $\pm$ 5.93 (0–28)	8.9 $\pm$ 15.10 (0–100)
3 Grasses (%)	0.2 $\pm$ 0.51 (0–2)	6.6 $\pm$ 18.37 (0–100)	0.8 $\pm$ 1.92 (0–5)**	26.6 $\pm$ 33.66 (0–100)	0.5 $\pm$ 1.42 (0–5)**	14.5 $\pm$ 27.39 (0–100)
4 Litter (%)	54.1 $\pm$ 22.22 (5–85)*	41.4 $\pm$ 25.38 (0–95)	51.9 $\pm$ 19.11 (20–80)**	35.2 $\pm$ 26.05 (0–95)	53.0 $\pm$ 20.45 (5–85)**	38.8 $\pm$ 25.81 (0–95)
5 Dead wood (%)	17.7 $\pm$ 11.40 (4–45)	15.1 $\pm$ 15.21 (0–95)	12.5 $\pm$ 11.01 (0–35)	8.4 $\pm$ 10.05 (0–80)	15.1 $\pm$ 11.35 (0–45)	12.4 $\pm$ 13.79 (0–95)
6 Rocks (%)	0.6 $\pm$ 1.89 (0–8)	0.5 $\pm$ 3.48 (0–80)	13.3 $\pm$ 7.48 (5–30)	8.9 $\pm$ 13.04 (0–90)	6.9 $\pm$ 8.42 (0–30)	3.9 $\pm$ 9.58 (0–90)
7 Bare ground (%)	16.4 $\pm$ 24.53 (0–85)	20.8 $\pm$ 21.64 (0–90)	5.6 $\pm$ 7.05 (0–20)	7.6 $\pm$ 10.08 (0–70)	11.0 $\pm$ 18.63 (0–85)	15.5 $\pm$ 19.07 (0–90)
8 Average hits at 1 m	1.38 $\pm$ 0.933 (0.25–3.00)	1.46 $\pm$ 1.738 (0–19.00)	0.97 $\pm$ 1.043 (0.00–4.00)*	4.53 $\pm$ 6.680 (0.00–53.00)	1.18 $\pm$ 0.997 (0.00–4.00)	2.68 $\pm$ 4.675 (0.00–53.00)
9 Percent closed	88.8 $\pm$ 10.41 (62–100)	79.7 $\pm$ 27.18 (0–100)	83.4 $\pm$ 12.83 (52–97)**	60.8 $\pm$ 34.45 (0–100)	86.1 $\pm$ 11.83 (52–100)**	72.2 $\pm$ 31.67 (0–100)
10 Slope (degrees)	3.3 $\pm$ 1.84 (0–7)	4.0 $\pm$ 6.13 (0–53)	12.7 $\pm$ 9.43 (1–31)*	8.2 $\pm$ 10.80 (0–52)	8.0 $\pm$ 8.23 (0–31)	5.6 $\pm$ 7.59 (0–53)
11 Total hits low	2.39 $\pm$ 2.593 (0–8)	3.52 $\pm$ 3.793 (0–25)	3.33 $\pm$ 2.657 (0–8)**	6.78 $\pm$ 4.650 (0–25)	2.86 $\pm$ 2.631 (0–8)**	4.82 $\pm$ 4.451 (0–25)
12 Total hits high	5.56 $\pm$ 2.770 (2–12)	5.67 $\pm$ 7.054 (0–50)	7.94 $\pm$ 8.606 (0–35)**	3.52 $\pm$ 6.157 (0–50)	6.75 $\pm$ 6.416 (0–35)	4.81 $\pm$ 6.792 (0–50)
13 Max. canopy height (m)	8.8 $\pm$ 2.94 (4.7–13.0)	7.4 $\pm$ 3.65 (0–30.00)	11.8 $\pm$ 7.57 (4.5–35.0)	8.9 $\pm$ 8.82 (0.0–35.0)	10.3 $\pm$ 5.86 (4.5–35.0)*	8.0 $\pm$ 6.29 (0.0–35.0)
14 Av. distance to nearest tree (m)	5.4 $\pm$ 2.34 (1.75–9.82)	5.8 $\pm$ 2.35 (0.75–10.00)	2.1 $\pm$ 1.07 (1.00–4.50)**	4.9 $\pm$ 2.93 (0.75–10.00)	3.8 $\pm$ 2.45 (1.00–9.82)**	5.4 $\pm$ 2.63 (0.75–10.00)

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

from abundance values, an estimate is needed of area sampled, taking into account the effective area of the grid outside the outer traps. For animals captured more than once, we calculated maximum distance moved between subsequent captures and took the average for all individuals trapped more than once. Following Wilson and Anderson (1985), we considered a border strip outside the outer traps to be equivalent to one-half the mean greatest distance traveled between successive points of capture, a value reported in Results. This was added to each side of the grid, and we considered grid corners to be rounded with a radius equal to the same value. The resulting effective area of each grid, 2.014 for males and 1.153 ha for females, was divided into abundance values to obtain density estimates (individuals/ha).

## Results

### General demographic characteristics

*Nyctomys sumichrasti* occurs throughout the state of Colima except possibly the southeastern part of the state (Fig. 1). Records are from our own sampling throughout Colima and from museum specimens collected by others. During 5 years (2003–2007) involving 40,000 trap-nights on grids, we captured 29 individuals a total of 41 times. Most captures were in arboreal traps (37 of 41; 90.2%). Except for 2007, most were adults, with subadults or juveniles encountered <18% of the time: 2003, 8 adults of 11 animals caught (72.7% adults); 2004, 1 adult (100.0%); 2005, 2 of 3 (66.7%); 2006, 7 of 8 (87.5%); and 2003–2006, 18 of 23 (78.3%). In 2007, one-third were adults, with one juvenile and three subadults in the six caught. For all years, 20 of 29 were adults (69.0%).

Numbers of adult *N. sumichrasti* of each sex and year were 2003, 4 males and 4 females (50.0% females); 2004, 0 and 1 (100.0%); 2005, 1 and 1 (50.0%); 2006, 4 and 3 (42.9%); 2007, 2 and 0 (0.0%); and all years, 11 and 9 (45.0%). Thus, fewer females than males were captured, except for 2004, when the only animal was a female. The sex ratio (males:females) of trapped individuals for all years was 1.22:1, not different from 1:1 (goodness-of-fit test,  $P=0.654$ ).

We recorded reproductive condition for the nine adult females. Numbers of females pregnant or lactating by year were 2003, 4 of 4 (100.0%); 2004, 0 of 1 (0.0%); 2005, 1 of 1 (100.0%); 2006, 2 of 3 (66.7%); and all years, 7 of 9 (77.8%). One of the active females in 2003 also had one young attached to a teat. The female in 2004 who was not reproductively active was postlactating, as was the inactive female in 2006.

Mean mass and SD for adult males and females were  $41.3 \pm 4.64$  g ( $n=11$ , range 35–50 g) and  $38.6 \pm 3.54$  g

( $n=9$ , range 35–45 g), respectively. Dimorphism in mass was not significant (one-way ANOVA,  $P=0.178$ ).

For each animal caught more than once, the mean and SD of greatest distance traveled between successive capture points was  $40.4 \pm 28.46$  m ( $n=8$ , range 10.0–92.2 m); the four males traveled farther on average ( $60.6 \pm 27.30$  m) than the four females ( $20.2 \pm 7.63$  m). Given that the eight animals for which we had data on greatest distance traveled were evenly divided by sex and location (coastal and northern Colima), we used a two-way ANOVA to evaluate possible differences due to these factors. Mean greatest distances moved ( $n=2$  for each group) were 81.4 m for coastal males; 16.2 m for coastal females, 39.6 m for northern males, and 24.2 m for northern females. Greatest distance traveled was not significantly different for location ( $P=0.122$ ) but highly significant for sex ( $P<0.01$ ). In addition, interaction between sex and location was significant ( $P=0.045$ ) reflecting that, while at both locations males moved farther than females, the intersex difference in distance moved was notably greater along the coast than in northern Colima. Means of greatest distances traveled for males and females were used to obtain 2.014 and 1.153 ha, respectively, as estimates of grid effective area (see Methods).

We captured *N. sumichrasti* on 9 of 25 grids, with 1–6/grid (Table 3). Abundance estimates based on minimum number of animals alive and effective grid areas for males and females ranged from 0.87–4.09/ha. Capture probabilities, assuming them to be equal across nights, were estimated (probability  $\pm$  SE with 95% confidence interval in parentheses) for four of the five years as follows: 2003,  $0.053 \pm 0.035$  (0.014–0.181); 2005,  $0.250 \pm 0.088$  (0.117–0.456); 2006,  $0.161 \pm 0.060$  (0.0750–0.313); and 2007,  $0.054 \pm 0.050$  (0.008–0.280). While variation among years is suggested, confidence intervals broadly overlap.

**Table 3.** Number of individual *Nyctomys sumichrasti* captured (i.e., minimum number alive) and density estimate for grids where the species was captured based on effective area of grid for males (2.014 ha) and females (1.153 ha).

Year	Grid	Minimum number alive		Density (number/ha)
		Males	Females	
2003	1	2	1	1.86
2003	3	1	1	1.36
2003	4	3	3	4.09
2004	2	–	1	0.87
2005	2	2	1	1.86
2006	1	2	2	2.73
2006	3	–	1	0.87
2006	4	2	1	1.86
2007	1	6	–	2.98

### Ecological characteristics comparing grids and trap stations

We evaluated means and SDs of environmental measurements on a grid level with one-way ANOVAs, contrasting the 9 grids where *N. sumichrasti* was captured with the 16 where it was not. No differences ( $P > 0.05$ ) were elicited for any of the 28 comparisons. The only variable approaching statistical significance was percent rocks ( $P = 0.068$ , average 2.37 vs. 6.61% for stations where captured and where not captured, respectively).

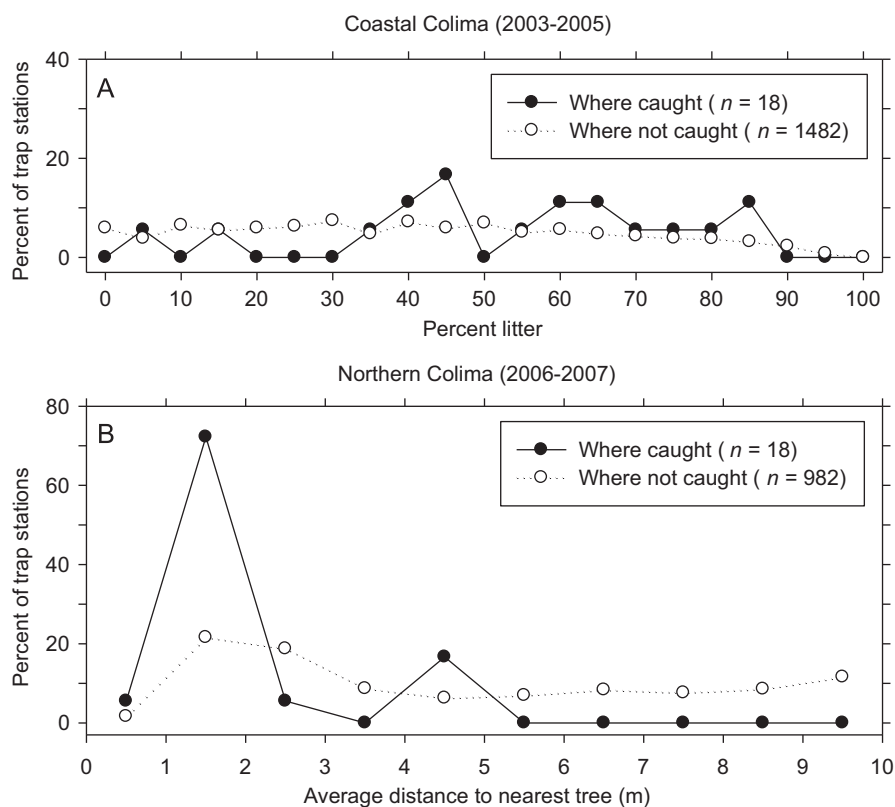
Mean values and SDs for the 14 vegetation-structure variables for trap stations where *N. sumichrasti* was caught and not caught are summarized in Table 2 for coastal grids, northern grids, and all years combined. When comparing variables for all years, six variables exhibited significant differences between stations where *N. sumichrasti* was caught and not caught (Table 2). Stations used by *N. sumichrasti* tended to have less grass, more litter, a more closed canopy, a more open understory, a higher canopy, and shorter distance to trees. For northern grid stations, eight variables were significant, with capture stations having less grass, more litter, fewer vegetation hits at 1 m, a more closed canopy, a steeper slope, a more open understory, more vegetation hits high, and shorter distance to trees. For

coastal-grid stations, significance was achieved for only percent litter, with capture stations having more litter.

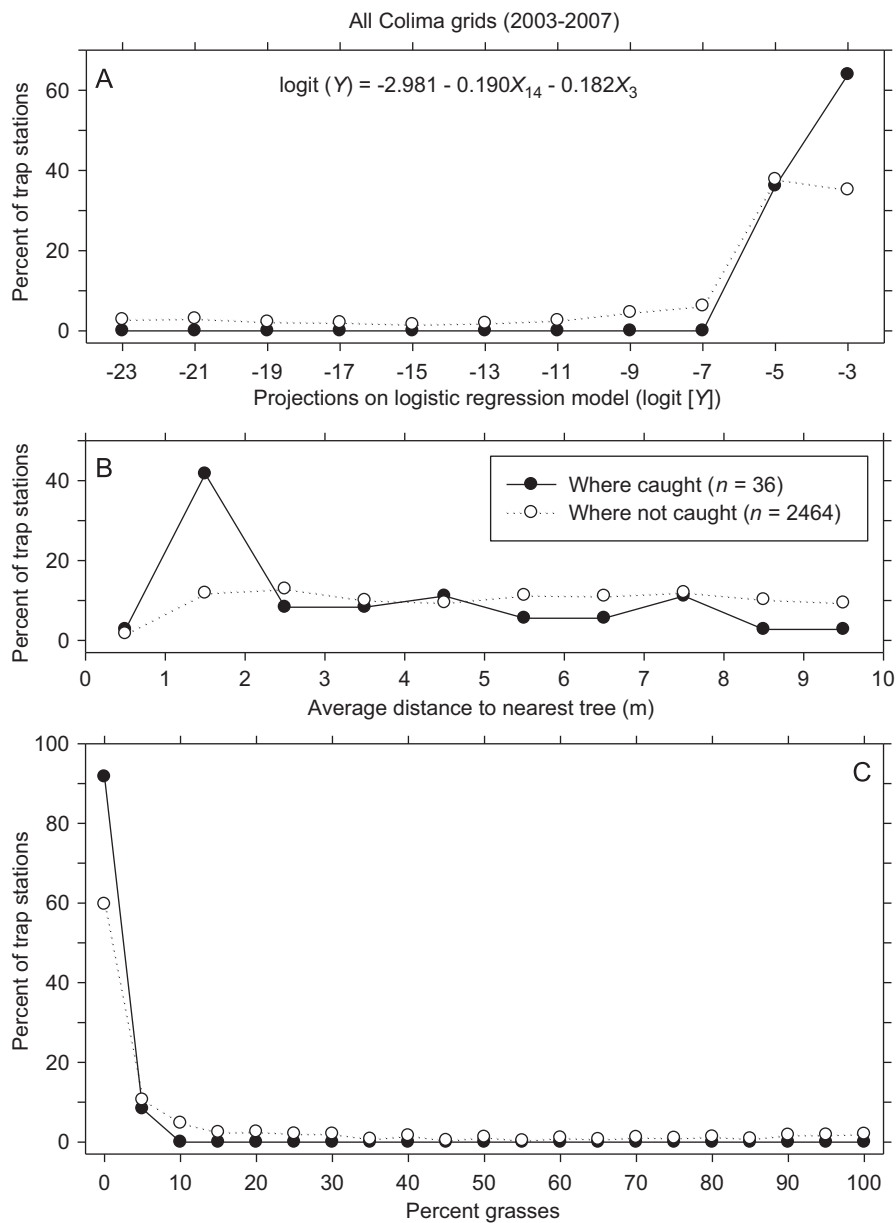
### Habitat evaluation using logistic regression

For coastal Colima, logistic regression of 1500 trap stations on 15 grids, contrasting those where *N. sumichrasti* was caught and not caught, yielded percent litter ( $X_4$ ) as the only predictive variable:  $\text{logit}(Y) = -5.370 + 0.020X_4$ , where the dependent variable  $\text{logit}(Y)$  is the natural logarithm of the odds of the species being present. McFadden's  $\rho^2$  for the model was only 0.024, indicating a weak model. Stations with *N. sumichrasti* tended to have more litter (Fig. 2A). For northern Colima, with 1000 trap stations on 10 grids, the equation was:  $\text{logit}(Y) = -1.895 - 0.693X_{14}$ , where  $X_{14}$  is average distance to nearest tree. McFadden's  $\rho^2$  was 0.125. In general, *N. sumichrasti* was captured where distance to trees was short (Fig. 2B).

Based on stations for all years combined, the equation was:  $\text{logit}(Y) = -2.981 - 0.190X_{14} - 0.182X_3$ , where  $X_{14}$  is average distance to nearest tree and  $X_3$  is percent grasses. McFadden's  $\rho^2$  was 0.083. Values of  $\text{logit}(Y)$  typically were higher for stations where the species was caught than where not encountered (Fig. 3A). Negative slopes for coefficients of the two independent variables



**Fig. 2.** Percentages of trap stations where *Nyctomys sumichrasti* was caught and not caught (A) on 15 grids in 2003-2005 in relation to percent litter at those trap stations and (B) on 10 grids in 2006-2007 relative to average distance to nearest tree.



**Fig. 3.** (A) Percentages of projections of trap stations in given classes for logistic-regression model based on data from all 25 grids (2003-2007) where *Nyctomys sumichrasti* was caught and not caught ( $X_{14}$  in model is average distance to nearest tree,  $X_3$  is percent grasses, and  $\text{logit}(Y)$  is the natural logarithm of the odds of the species being present). (B) Percentages of trap stations where *N. sumichrasti* was caught and not caught in 2003-2007 relative to average distance to nearest tree. (C) Percentages of trap stations where *N. sumichrasti* was and was not caught in relation to percent of ground cover that was grass.

indicate *N. sumichrasti* preferred areas with little grass (Fig. 3C) where distance to trees was short (Fig. 3B).

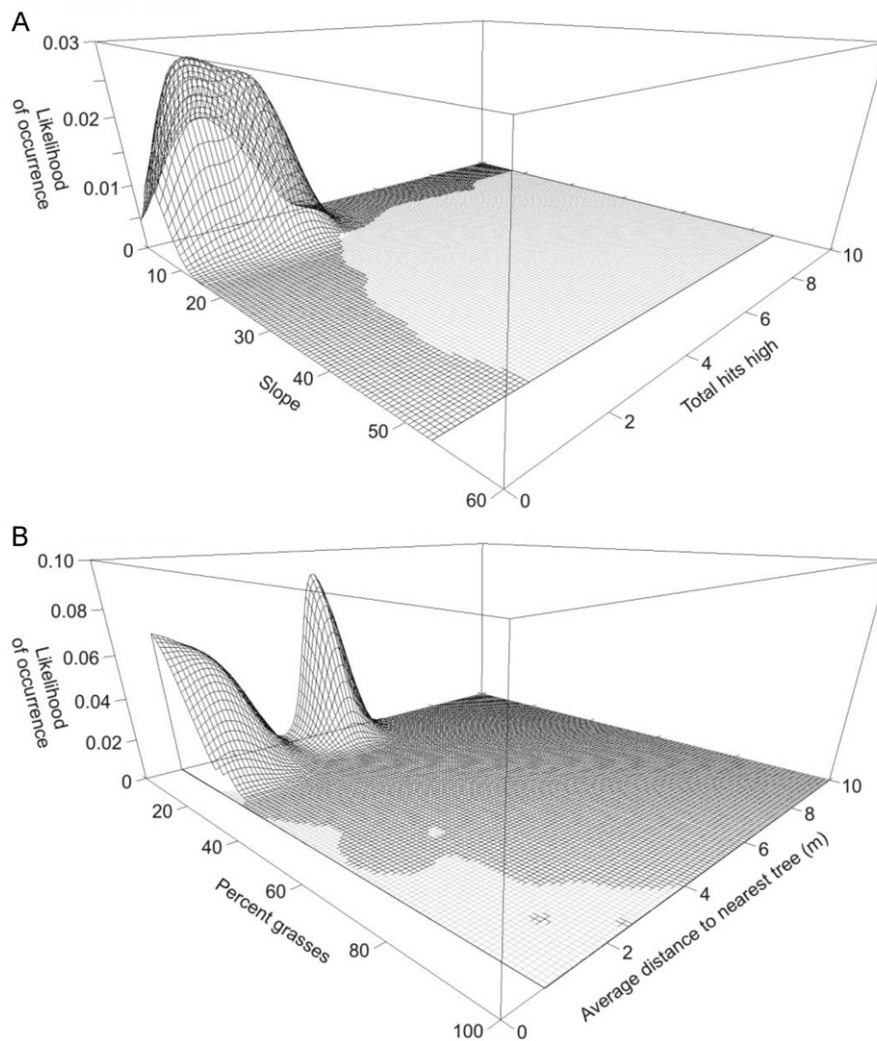
**Habitat evaluation using nonparametric multiplicative regression**

Using NPMR for coastal Colima, two variables—total hits high and slope—were incorporated in the best model (Fig. 4A, Table 4). Likelihood of occurrence of *N. sumichrasti* was greater than zero only when total hits

high were 0-10 and slopes  $\leq 15^\circ$  (Fig. 4A). Even in areas with this combination, likelihood of occurrence seldom was  $> 0.025$ . Given particular combinations of characteristics at the 1500 stations in coastal Colima, data were insufficient to evaluate likelihood of occurrence for combinations of total hits high  $> 10$  and slopes  $> 15^\circ$  (i.e., gray area in Fig. 4A); however, it is highly unlikely that *N. sumichrasti* would ever occur in such areas, even if they existed.

The best NPMR model for northern Colima also included two variables—average distance to nearest tree





**Fig. 4.** (A) For coastal Colima (2003–2005), three-dimensional representation of best NPMR model, which included two variables, indicating likelihood of occurrence of *Nyctomys sumichrasti* relative to slope and total hits high. (B) For northern Colima (2006–2007), likelihood of occurrence of *N. sumichrasti* relative to average distance to nearest tree and percent grasses. Grayed portions of graphs indicate regions where data were insufficient to make a reliable estimate of likelihood of occurrence.

and percent grasses (Fig. 4B, Table 4). There was virtually no likelihood that *N. sumichrasti* would occur in habitats with ground cover >30% grasses. For average distance to nearest tree, the likelihood function was bimodal, with highest likelihoods of *N. sumichrasti* occurring when average distances to nearest tree were about 1 m and 3 m (Fig. 4B).

When considering all grids, the best model included four variables—percent grasses, percent rocks, slope, and average hits at 1 m (Table 4). In Fig. 5, the first two variables are depicted in panel A and the latter two in panel B. There is little likelihood of finding *N. sumichrasti* if ground cover has >20% grasses or >30% rocks (Fig. 5A). Also, the species would almost never occur in places where average vegetation hits at 1 m on a 1-m vertical bar were >10 (Fig. 5B). For slope, likelihood of occurrence is shown as a trimodal function,

with no probability of the species being present with slope >30°; the trimodal aspect may in part be an artifact of sampling, but our Colima data indicate the species does not frequent steep slopes. Overall, the model suggests *N. sumichrasti* tends to occur where ground cover includes little grass and few rocks, slope is flat to moderate, and understory is relatively open a meter or so above the ground.

## Discussion

### General demographic characteristics

In Nicaragua, Genoways and Jones (1972) collected 11 adult males and 22 adult females, with 40 males and

**Table 4.** Best NPMR models for given number of predictors to estimate likelihood of occurrence of *Nyctomys sumichrasti* for 15 coastal Colima grids (18 stations where caught and 1482 where not caught), 10 northern grids (18 stations where caught and 982 where not caught), and all grids (36 stations where caught and 2464 where not caught). Results were such that models with two or more variables simply involved addition of a variable to previous set; this need not be the case because models are generated independently. Models with greatest number of variables were judged to be best overall.

Number of variables	Log <i>B</i>	$\Delta$ log <i>B</i> from previous model	Average neighborhood size	Variables (tolerance)
<b>Coastal Colima (2003-2005)</b>				
1	1.0926		583.60	Total hits high (2.50)
2	2.3805	1.2879	305.74	Slope (2.65)
<b>Northern Colima (2006-2007)</b>				
1	5.8762		146.49	Av. distance to nearest tree (0.46)
2	7.4779	1.6017	69.92	Percent grasses (5.00)
<b>All Colima grids (2003-2007)</b>				
1	4.3471		1195.89	Percent grasses (5.00)
2	6.9724	2.6253	785.46	Percent rocks (4.50)
3	9.3425	2.3701	397.07	Slope (2.65)
4	9.6085	0.2660	301.31	Average hits at 1 m (2.62)

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

43 females obtained in all age classes. Fleming (1970) recorded a male:female sex ratio of 1.62:1 in Panama, consistent with our finding of 1.22:1, although neither differs statistically from 1:1. Thus, available data—albeit limited—suggest populations of *N. sumichrasti* do not deviate from a 1:1 sex ratio. This conclusion rests on an assumption that there is not trap or collection bias contributing to more frequent captures of males or females, an assumption not tested to date for *N. sumichrasti*. Our finding that males move farther than females does not necessarily indicate a trap or collection bias with respect to sex.

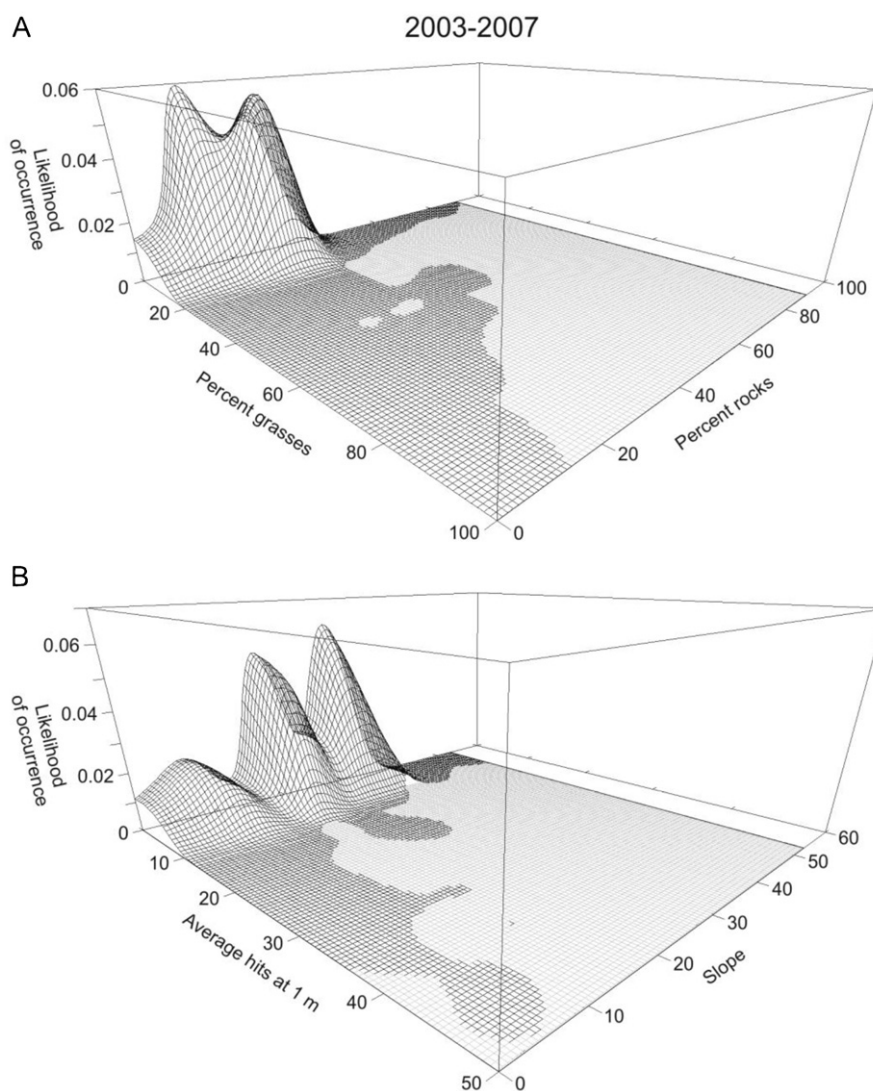
*Nyctomys sumichrasti* likely is a year-round breeder, despite the large variation that comes with the wet and dry seasons in most of their habitats. In Panama, Fleming (1970) caught reproductively active females in February, March, and June, as well as juveniles from March-May. Genoways and Jones (1972) caught animals of all age classes in both wet and dry seasons. Timm and Vriesendorp (2003) mentioned a *N. sumichrasti* in Costa Rica in January 1999 had clearly visible, enlarged teats, complementing our own results showing the species is reproductively active in the dry season in January. Sánchez-Hernández et al. (1999) captured a pregnant female in Michoacán in June. Over the 5 years of our January studies, 77.8% of adult females were lactating or pregnant, with the others being postlactating.

Body mass for *N. sumichrasti* has seldom been reported. Genoways and Jones (1972) noted a significant difference (3.6 g) in mean mass of males (48.5 g)

and females (44.9 g) in Nicaragua. For 15 linear measurements, none were sexually dimorphic. On average, males in our study were heavier than females (difference 2.7 g), although not significantly so.

In Panama (Fleming, 1970), average greatest distance moved between successive capture sites was 60 m for three females and 131 m for a male, values even longer than ours (20.2 and 60.6 m, respectively). In Jalisco, Domínguez Castellanos (2006) established four grids (10 × 10 trap stations) with three traps per station (1, 2, and 2.5 m above ground). Animals marked with fluorescent powder were released at 0300 h and movements for the rest of the night discerned using a fluorescent lamp. Seven female *N. sumichrasti* moved 7.2–29.4 m and 12 males 5.2–49.5 m, with the mean for the 19 individuals being 16.2 m. These movements were for a portion of single nights and, thus, not surprising tend to be shorter than those we obtained; some of our findings were based on subsequent trappings > 1 night apart.

We had 16 trap grids where *N. sumichrasti* was not captured, with densities of 0.87–4.09/ha on the other 9 grids. Our density estimates, based on minimum number known alive, produced values that could be considerably lower than actual densities. In particular, because our arboreal traps were 1–2 m above the ground, we probably missed some animals that did not descend from higher parts of the vegetation. In off-grid traps we caught *N. sumichrasti* as high as 15 m above ground and suspect that some regularly spend time even higher in trees. Over a 5-month period, Fleming (1970)



**Fig. 5.** Four variables included in best model when considering all stations for both coastal and northern grids. Likelihood of occurrence of *Nyctomys sumichrasti* estimated relative to: (A) percent grasses and percent rocks; and (B) average hits at 1 m and slope. Grayed portions of graphs indicate regions where data were insufficient to make a reliable estimate of likelihood of occurrence.

caught 34 individuals, with a high of 15 animals in January and lows of 3 in May and 2 in June. His supposition was that population size had not changed dramatically but variance was due to a change in food supply; he suggested because natural foods (e.g., palm nuts and fruit) were scarce November–February, *N. sumichrasti* in December were using traps as a food source, resulting in many more being caught. As we did, Ceballos (1990) used minimum number of individuals known to be alive to estimate abundance. He caught five *N. sumichrasti* on three 0.5-ha grids.

In-depth and long-term mark-and-recapture studies of *N. sumichrasti* would be of interest. It may be a species that simply does not occur in high densities. However, most trapping schemes for small mammals that spend most of their time close to the ground are not

optimal for sampling highly arboreal species. Ceballos and Miranda (1986) pointed out the difficulty of estimating abundance and density of *N. sumichrasti* given its highly arboreal nature.

### Behavior

Our captures of *N. sumichrasti* were mostly in arboreal traps (90.2%), similar to findings of others (Fleming, 1970; Genoways and Jones, 1972; Timm and Vriesendorp, 2003). Animals in a 13-month laboratory study spent much of their time perched on branches or hanging on sides of cages—sometimes only with their back feet—performing activities such as eating and grooming (Birkenholz and Wirtz, 1965). Ceballos and

Miranda (1986) referred to *N. sumichrasti* as a strictly arboreal species, and Ceballos (1990) had five captures of *N. sumichrasti*, all in arboreal traps. However, *N. sumichrasti* is not exclusively arboreal, as indicated by almost 10% of our captures and 21% of those by Fleming (1970) being in ground traps. Genoways and Jones (1972) also caught some of their nearly 100 specimens in traps placed at bases of trees.

The species has extensive vertical range. Ceballos (1990), Timm and Vriesendorp (2003), and Disney (1968) noted *N. sumichrasti* at heights of 0.7–7 m, 7 m, and 0–8 m, respectively. It comprised 0.2% of species caught on the ground in a study of leishmaniasis (*Leishmania mexicana*) but contributed 13.1% to total animals captured in traps placed at 0–4 m elevation and 19.0% for those set at 4–8 m (Disney, 1968). Genoways and Jones (1972) observed *N. sumichrasti* in the lower story of vegetation during the wet season but in the dry season many were much higher, especially when feeding in fig trees. As noted, we trapped the species as high as 15 m above the ground in January in addition to capturing it in grid traps 1–2 m above ground.

We caught one female twice, both times with a young attached to her teat. It has been posited that teat attachment is an adaptation related to being arboreal (Birkenholz and Wirtz, 1965; Ceballos, 1990). Young of this species spend most of their first two weeks of life attached this way (Birkenholz and Wirtz, 1965), and Ceballos (1990) reported two females maintained in the laboratory having young attached for the first five weeks of life. Young typically do not leave the nest attached to the mother unless she is forced out (Birkenholz and Wirtz, 1965).

## Ecological characteristics

*Nyctomys sumichrasti* has been recorded in arid, wooded mountain slopes in Oaxaca and humid areas in northern Oaxaca (Goodwin, 1969), evergreen forest of central and western Panama (Handley, 1966), second-growth, dry tropical forests in coastal Panama interspersed with grassy corridors (Fleming, 1970), and in dense second-growth scrub forest in Nicaragua along a small stream and cloud forest where understory was cleared for agriculture (Jones and Genoways, 1970). In Costa Rica, it was in premontane/lower montane wet forest (Timm and Vriesendorp, 2003). The first specimen of *N. sumichrasti* was collected in a cane thicket on the eastern slope of mountains in Veracruz (Sumichrast, 1882, Alvarez, 1963), and Ceballos (1990) conducted his study in an ecosystem featuring deciduous and arroyo forests in Jalisco. Sánchez-Hernández et al. (1999) caught one near a stream in a tropical subdeciduous forest in Michoacán. *Nyctomys sumichrasti* was present in the forests of the Cayo District of Belize (Disney,

1968); they avoided nearby developed land and pine savannah.

Reid (2009) indicated that *N. sumichrasti* has been found in evergreen and semideciduous forest and tall second growth, while Emmons (1997) noted that it typically occurs in evergreen lowland and lower montane forests, old secondary and riparian forests, and semideciduous forests. We sampled a range of habitats in Colima, but with grids mostly in woodlands, where *N. sumichrasti* generally occurred in places with more litter, less grass, a more closed canopy, fairly open understory, and closer trees. In coastal Colima, the logistic-regression model was not particularly robust but indicated that the species tended to be in areas with more litter. The NPMR model for coastal Colima detected only two predictive characters—few hits high and a slope <15°. For northern Colima, however, the NPMR model echoed our other evaluations in showing low amounts of grass and close-standing trees to be good predictors for *N. sumichrasti*.

In forest interspersed with grassy corridors, Fleming (1970) found *N. sumichrasti* only in wooded portions, often in areas with dense vegetation. Genoways and Jones (1972) encountered *N. sumichrasti* in Nicaragua in riparian habitat bordering sugarcane fields; the area around the stream had dense understory composed of small trees, shrubs, and vines, and a second-story canopy of tall tropical trees reaching up to about 30 m in height. These descriptions fit well with some of our findings—close trees and a tall, closed canopy, with *N. sumichrasti* avoiding grassy areas. However, their results differ from ours in that we found understory to be relatively open in areas with *N. sumichrasti* present. Hunt et al. (2004) reported *N. sumichrasti* in a cloud forest with cleared understory, a result agreeing well with our quantitative vegetation analyses.

Our results and those of others clearly indicate that *N. sumichrasti* selects forest habitat and sharply avoids open areas. Throughout its range, the species favors areas relatively dense in tall trees. It tolerates areas with dense understory, as was the case in Nicaragua (Genoways and Jones, 1972) and Panama (Fleming, 1970). Our findings suggest that *N. sumichrasti* favors more open understory, at least in some parts of Colima. It would be of interest to include adjacent areas with high and low understory densities in any further studies of this species.

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## Appendix

Gazetteer of localities in Colima, Mexico, where *Nyctomys sumichrasti* has been recorded. Locality numbers refer to those in Fig. 1, where in two cases geographically close localities are represented by a single symbol; below they are so identified with addition of a lowercase letter to the locality number. Each listing indicates the municipality before providing specific locality information.

(1) Minatitlán, Rastrojitos, 3 km NW Ranchitos, 1650 m. (2) Cuauhtémoc, Rancho La Angostura, 761 m, 19°18.837'N, 103°39.997'W. (3) Cuauhtémoc, 6 km S Cuauhtémoc, 710 m, 19°16.083'N, 103°36.000'W. (4) Cuauhtémoc, airport of Colima, 19°16'12.5''N, 103°35'33.4''W. (5) Coquimatlán, Pueblo Juárez, 6 km N Agua Zarca. (6) Coquimatlán, Pueblo Juárez, 19.0833°N, 103.833°W. (7) Coquimatlán, La Fundición, 19°08.498'N, 104°01.179'W. (8) Manzanillo, 4 km E Don Tomás, 19°12'51''N, 104°22'03''W. (9a) Manzanillo, Playa de Oro, 19°08.102'N, 104°29.917'W. (9b) Manzanillo, Playa de Oro, 3 m, 19°07.947'N, 104°30.802'W. (10) Manzanillo, Agua Blanca, 141 m, 19°03.961'N, 104°03.152'W. (11a) Colima, El Hervidero, 5 km S de Puerta de Anzar, 244 m, 19°04'54''N, 103°32'18''W. (11b) Colima, 1 km E de El Hervidero, 5 km S de Puerta de Anzar, 19°04.854'N, 103°32.153'W.

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