*Demographic features, distribution, and habitat selection of the gray mouse opossum (*Tlacuatzin canescens*) in Colima, Mexico*

Michael L. Kennedy, Gary D. Schnell, María de Lourdes Romero-Almaraz, Bahar S. Malakouti, Cornelio Sánchez-Hernández, et al.

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Demographic features, distribution, and habitat selection of the gray mouse opossum (*Tlacuatzin canescens*) in Colima, Mexico

**Michael L. Kennedy · Gary D. Schnell ·
María de Lourdes Romero-Almaraz ·
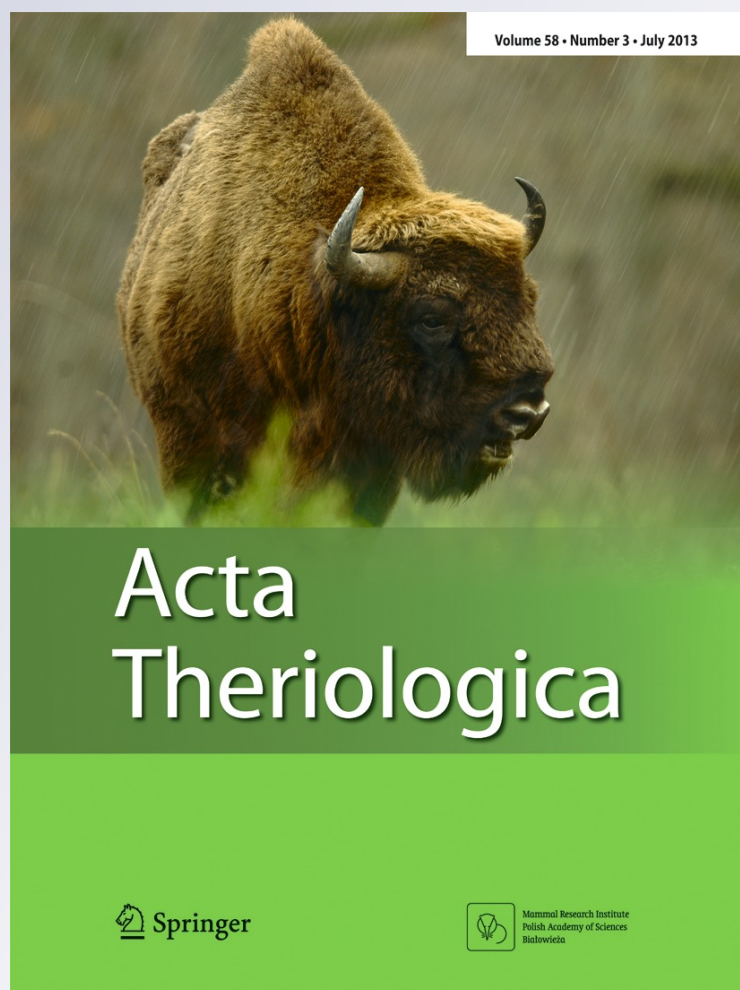Bahar S. Malakouti · Cornelio Sánchez-Hernández ·
Troy L. Best · Michael C. Wooten**

Abstract In western Mexico, gray mouse opossums *Tlacuatzin canescens* typically are not only in tropical deciduous and semideciduous woodlands but also in croplands and orchards. We conducted mark-recapture studies in January 2003–2007 and 2010 in coastal, northern, and central Colima, Mexico. Each year, five grids, established in areas of thick vegetation within a mosaic of habitats, had 100 stations (10×10), each with two Sherman traps, one on the ground and another elevated 1–2 m. On 24 of 30 grids, 82 individuals were captured 126 times (85.7 % in elevated traps). Sex ratio did not deviate from 1:1; there was no sexual dimorphism in mass (average for males, 28.21 g; average for females, 25.64 g); 46.3 % of animals were adults, 27.3 % of adult females were reproductively active, and 77.5 % of males had scrotal testes. Distance from centroid of trap locations averaged 15.24 m, with mean minimum distance moved between captures being 33.19 m. Densities usually were low (0.67–8.03/ha), with the species widespread in habitats studied. We assessed 14 environmental characteristics for each station using ANOVA, logistic regression, and nonparametric multiplicative regression (NPMR) to characterize habitat selection. *T. canescens* was more likely found where percent grass was about 30 % and litter over 50 %, with height of canopy less than 10 m and about 40 % closed. NPMR, being able to recognize hump-shaped response curves where intermediate variable values are preferred, identified two variables (percent grass and percent canopy closed) not detected by other techniques as important in characterizing habitat selection of *T. canescens*.

Keywords Didelphidae · Didelphinae · HyperNiche · Logistic regression · Nonparametric multiplicative regression · Population density

M. L. Kennedy
Ecological Research Center, Department of Biological Sciences, University of Memphis, Memphis 38152, USA

G. D. Schnell (✉) · B. S. Malakouti
Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of Oklahoma, 2401 Chautauqua Avenue, Norman, OK 73072, USA
e-mail: gschnell@ou.edu

M. d. L. Romero-Almaraz
Escuinapa No. 92 bis. Col. Pedregal de Santo Domingo, 04369, Mexico, DF, Mexico

C. Sánchez-Hernández
Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, 04510 Del. Coyoacán, Mexico, DF, Mexico

T. L. Best · M. C. Wooten
Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849, USA

Introduction

The gray mouse opossum *Tlacuatzin canescens* is endemic to Mexico and occurs in tropical lowlands from southern Sonora to Oaxaca, northeastern Yucatán, the Tres Marías Islands, and possibly Baja California Sur (Gardner 2005; Hernández-Cardona et al. 2007). Previously, the species was in the genus *Marmosa*, but based on morphological and karyotypic characteristics, Voss and Jansa (2003) placed the species in *Tlacuatzin*. The smallest opossum in Mexico, *T. canescens* is known from elevations of 0–2,100 m but most occurs at elevations of <1,000 m (Zarza et al. 2003).

Typically, *T. canescens* inhabits tropical and semideciduous forest with notable wet–dry seasonality along the Pacific coast. The species has been characterized as being omnivorous, semiarboreal, and nocturnal. While general

ecology of *T. canescens* has been treated briefly by a number of authors (e.g., Hall and Villa-R 1949; Ceballos and Miranda 2000), habitat selection has not been evaluated in detail. *T. canescens* has been described as inhabiting all vegetation types, including perennial crops where natural vegetation has been replaced by plantations of bananas (*Musa*), mango (*Mangifera*), and coconut (*Cocos*) (Ceballos and Miranda 2000).

There are few reports on demography or population size for the species. Much of the range of *T. canescens* is in a region considered to be a biodiversity hotspot (Shi et al. 2005) and potentially at risk (Sánchez-Azofeifa et al. 2005). Sánchez-Cordero et al. (2005) noted that as of 2000, almost 40 % of habitat potentially used by *T. canescens* had been transformed through deforestation.

We have studied demography and ecology of *T. canescens* in Colima, Mexico. Our objectives were (a) to evaluate habitat use and selection by *T. canescens* during the dry season, comparing results emanating from different analytical approaches; (b) to record basic demographic features; (c) to estimate population density; and (d) to obtain information of movements by males and females.

Materials and methods

Study areas and trapping protocol

Our study was conducted in coastal, northern, and central Colima. The coastal site was adjacent to the Pacific Ocean at Playa de Oro (Fig. 1, locality 3) and was used in January 2003, 2004, and 2005. Northern localities, evaluated in January 2006 and 2007, were in the vicinity of Miguel de la Madrid Airport (locality 20) and at Rancho La Angostura (19.3139500° N, 103.6666167° W; location shown by open square in Fig. 1). In January 2010, the study site was 3 km east of Los Asmoles (locality 22 in central Colima).

The coastal study area at Playa de Oro was within 1 km of the ocean with elevations of <10 m above sea level (asl). As described by Schnell et al. (2008) in a parallel study of the southern pygmy mouse *Baiomys musculus*, habitat at Playa de Oro was primarily tropical dry deciduous forest, with thorn-forest and mangrove elements. Prominent trees and shrubs included *Coccoloba barbadensis*, several *Acacia* (including *Acacia hindsii* and *Acacia farnesiana*), *Senna pallida* and *Senna occidentalis*, *Pithecellobium lanceolatum* and *Pithecellobium dulce*, *Hyperbaena ilicifolia*, *Crataeva tapia*, *Prosopis juliflora*, and *Guazuma ulmifolia*. Grazing occurred in the area, but large portions of our grids were inaccessible to livestock due to thick vegetation. Prominent agriculture in the vicinity of our study plots included groves of coconut palms *Cocos nucifera* and production of corn *Zea mays*, sweet potatoes *Ipomoea batatas*, and beans *Phaseolus vulgaris*.

The northern Colima study sites at Rancho La Angostura and in the vicinity of Miguel de la Madrid Airport were at elevations of 700–765 m asl. Vegetation on grids at Rancho La Angostura was tropical moist forest (i.e., tropical sub-deciduous forest), with overall landscape being fragmented and mostly used for cultivated agriculture (mainly oranges and limes; *Citrus*) and raising livestock. Some areas along water courses retained gallery forest and native vegetation. Habitat sampled was heavily shaded gallery forest with open understory and trees 5–40 m in height; numerous species of trees were present, the most abundant in this type of forest being *Alnus*, *Salix humboldtiana*, *Salix bonplandiana*, *Cecropia obtusifolia*, *Ficus* spp., and *Inga eriocarpa* (Schaldach 1963). A low-density coffee-tree *Coffea arabica* plantation was situated below the canopy of trees.

The area adjacent to Miguel de la Madrid Airport (locality 20) had been highly fragmented and used for agriculture in the past, but was fenced, protected, and left relatively undisturbed for about 30 years prior to our investigation. Much of the study area had reverted to tropical moist forest intermixed with grass-dominated habitat (*Andropogon*; often >2 m in height). Characteristic trees were *Brosimum alicastrum*, *Sideroxylon cartilagineum*, *Coussapoa purpusii*, *Hura polyandra*, *Guarea glabra*, *Dendropanax arboreus*, and *Populus guzmanantlensis* (Schaldach 1963).

At the central Colima site near Los Asmoles, grids were in relatively thick vegetation varying from being dominated by dense trees to grassy fields with scattered trees and bushes. Grids 1 and 2 had few trees, with much of the vegetation no more than 1.5 m high. Trees included *Acacia farnesiana* and *Melia azedarach*, and *Caesalpinia cacalaco*. Other characteristic plants were *Melochia pyramidata*, *Ricinus communis*, *Senna uniflora*, *Malvastrum americanum*, *Lagascea aurea*, and *Lopezia racemosa*. Grids 3–5 were in dry thorn forest with scattered patches of maguey *Agave* (Agavaceae) throughout each grid. Trees included *Cescentia alata* and *Lysiloma microphylla*. Other plants on these grids were *Elytraria imbricata*, *Gossypium aridum*, and *Bastardiastrum incanum*. Steep slopes were present on grids 3–5 and areas with thick understory alternated with places that were more open.

Trapping sessions were in January of each year during the annual dry season. Typically, at this time of year, days are warm and nights cool. The average January temperature for Manzanillo, 21 km east-southeast of the coastal study site, was 24.8 °C and monthly rainfall 7.8 mm, with parallel values for northern Colima (Miguel de la Madrid Airport) being 24.1 °C and 10.6 mm (averages 1993–2010; http://clima.tiempo.com). Temperatures at the central Colima site were similar to those for northern Colima, and rainfall averaged somewhat lower. There was little day-to-day variation in temperature during our studies and no rain, except in 2010. Relatively little variation in temperature or rainfall
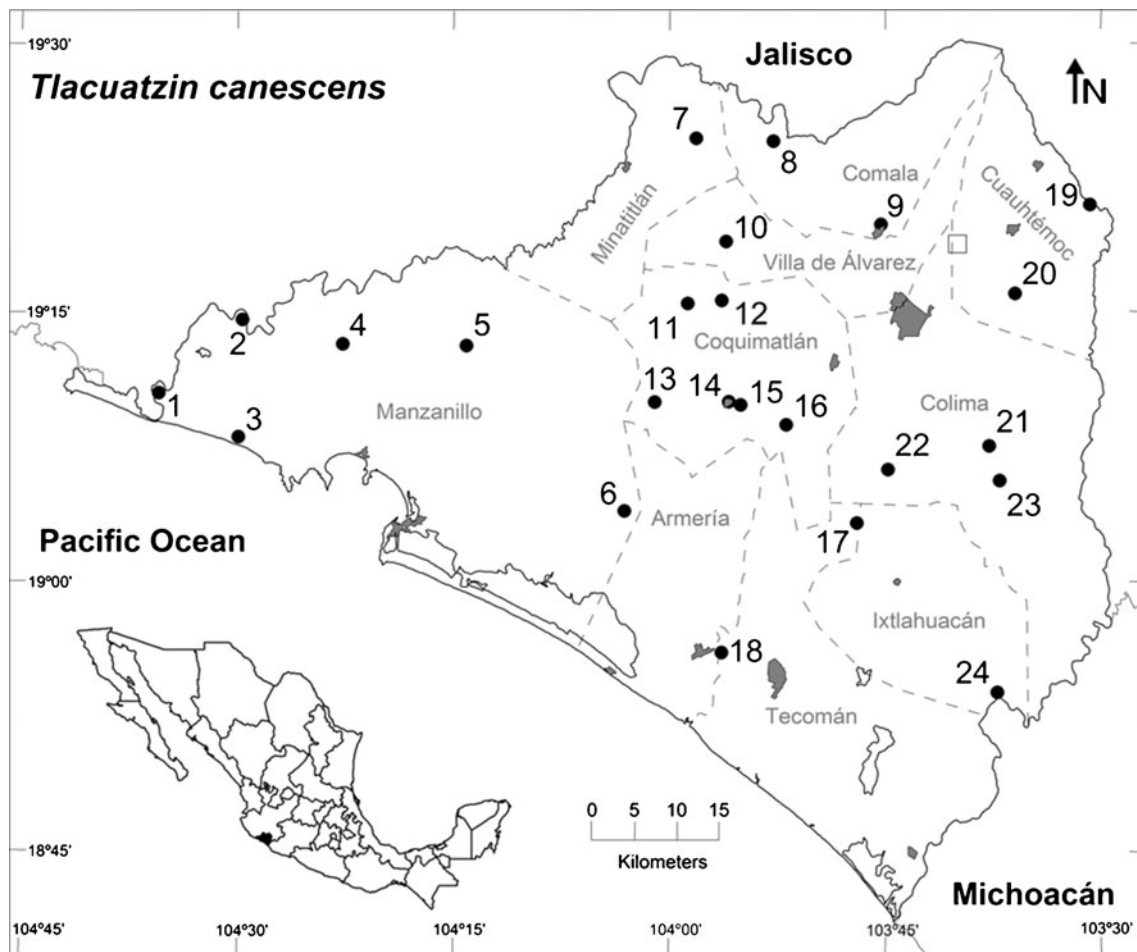
Fig. 1 Locations in state of Colima where *Tlacuatzin canescens* has been captured (number 14 on map represents two geographically close localities). Locality numbers are referenced in the gazetteer (Appendix), which includes more detailed information. *Inset map* indicates position of Colima in Mexico. Grids in coastal Colima in 2003–2005 were at locality 3. In northern Colima in 2006–2007, grids where we had captures were at locality 20. *Open square* represents location of La Angostura, where grids were set in 2006 but *T. canescens* was not captured. In central Colima in 2010, grids were at locality 22. Bodies of water are shown (*outlined*), as are some cities and towns (*shaded*). *Dashed lines* indicate boundaries of ten municipalities in Colima, which are named after principal city or town in each

occurred from year to year. For example, at the Airport for 2003–2007 and 2010, average of January average temperatures was 25.3 °C, with a range from 23.8 (2004) to 26.1 °C (2003). The average of monthly precipitation for 2003–2007 and 2010 was 7.8 mm, with a range from 0 (four of the years) to 60.4 mm (2004); in the latter case, most rainfall was during one night in the month, with our study having been completed before that rainfall. With a decided dry season (November–May), annual precipitation on average was 946 mm for Playa de Oro, 1,152 mm for Miguel de la Madrid Airport, 1,080 mm for Rancho La Angostura, and 810 mm for Los Asmoles (1960–1990; http://www.worldclim.org).

Five trapping grids were established each year (30 total for the 6 years). Grids at a given locality did not overlap spatially and, in a given year, adjacent grids were never closer than 500 m. Grids were situated in trapping locations so as to encompass the various types of vegetation present in the immediate area (Table 1). Each grid consisted of 100 trapping stations (10×10 grid), with adjacent stations being 10 m apart. Two Sherman live traps ($7.5 \times 9.0 \times 23.0$ cm; H.B. Sherman Traps, Tallahassee, Florida) were placed at each station, one on the ground and another 1–2 m above ground on a thin plywood platform (12.5×34.5 cm) attached to a tree or shrub (hereafter referred to as elevated traps). Traps were baited with rolled oats. In all but two instances, grids were sampled for eight nights (Table 1); the exceptions were grid 5 in 2004, which was evaluated for nine nights, and grid 1 in 2005, which was checked for seven nights. Relatively few "new" animals were captured at the end of a given sampling period, so extending an additional night or having one less night had little effect. Overall, sampling effort on grids involved 48,000 trap nights (one trap night=one trap set for one night).

We checked traps daily starting at dawn, rebaited them as needed, and left them open for the full 24-h period. When an

Table 1 General description of grids in state of Colima, Mexico, with sampling dates in January (modified from Schnell et al. 2008)

Grid number (January dates)	General description
2003 (coastal Colima)	
1 (2–5 and 9–12)	Thorn forest with some palm trees in proximity to mangroves
2 (2–5 and 9–12)	Thorn forest with some palm trees in proximity to mangroves
3 (3–5 and 9–13)	Thorn forest adjacent to palm plantation
4 (3–5 and 9–13)	Thorn forest adjacent to palm plantation
5 (3–5 and 9–13)	Mixture of grassy patches and palm trees associated with undergrowth of thorn forest
2004 (coastal Colima)	
1 (3–5 and 9–13)	Mixture of thorn forest and mangrove, with some palms
2 (2–5 and 9–12)	Mixture of thorn forest and mangrove, with some palms
3 (2–5 and 9–12)	Thorn forest in proximity to palm plantation
4 (3–5 and 9–13)	Mixture of grassy patches, palm trees, and thorn forest adjacent to agricultural fields
5 (3–5 and 9–13)	Mixture of grassy patches, palm trees, and thorn forest adjacent to agricultural fields
2005 (coastal Colima)	
1 (4–6 and 10–13)	Dense thorn forest with abundance of woody vines
2 (3–6 and 10–13)	Thorn forest mixed with mangrove and palm trees with dense undergrowth
3 (2–6 and 10–12)	Mixture of thorn forest, grassy patches, and xerophilous scrubs
4 (2–6 and 10–12)	Mixture of grassy patches, palm trees associated with dense undergrowth of thorn forest, and patches of mangrove
5 (3–6 and 10–13)	Mixture of grassy patches, palm trees, and thorn forest
2006 (northern Colima)	
1 (2–6 and 10–12)	Tropical deciduous forest with tall, mature trees and dense understory, bordered by small stream
2 (2–6 and 10–12)	Tropical deciduous forest with tall, mature trees and dense understory, bordered by small stream
3 (3–6 and 10–13)	Thorn forest with sparse understory vegetation intermixed with patches of tall grass (height 1.0–1.5 m)
4 (3–6 and 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 and 10–13)	Thorn forest with sparse understory vegetation intermixed with patches of tall grass (height 1.0–1.5 m)
2007 (northern Colima)	
1 (2–6 and 10–12)	Tropical deciduous forest with some mature trees, sparse understory with some young thorn trees (partially cleared, unimproved road traversed grid)
2 (2–6 and 10–12)	Mixture of tropical deciduous with large, mature trees and thorn-forest elements
3 (2–6 and 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 and 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 and 10–13)	Tall dense grasses (1.0–3.0 m) with isolated trees
2010 (central Colima)	
1 (3–6 and 10–13)	Field on level ground with tall grasses and scattered trees and bushes
2 (3–6 and 10–13)	Field on level ground with tall grasses and scattered trees and bushes
3 (2–6 and 10–12)	Tropical deciduous forest with some mature trees, thorn-forest elements, and varied understory. Included scattered, thick patches of maguey
4 (2–6 and 10–12)	Tropical deciduous forest with some mature trees, thorn-forest elements, and varied understory. Included scattered, thick patches of maguey
5 (2–6 and 10–12)	Tropical deciduous forest with some mature trees, thorn-forest elements, and varied understory. Included scattered, thick patches of maguey

For 2003–2005, all grids at locality 3 (Fig. 1). For 2006, grids 1–2 at La Angostura (open square) and grids 3–5 at locality 20. In 2007, all at locality 20 and, in 2010, all at 22

animal was captured, we recorded position of trap (i.e., location in grid and ground vs. elevated), sex, reproductive condition or condition of reproductive organs, and age (adult, subadult, or juvenile). For reproductive condition in adult males, we recorded whether testes were scrotal or not descended. Our studies were conducted at the end of the

reproductive season. For adult females, we tabulated whether they had been reproductively active (i.e., postlactating as indicated by no hair around elongated nipples) or had not been active (i.e., hair around short nipples) during the previous reproductive period. Age was judged on the basis of mass (ca. adults, ≥20 g; subadults, ≥15 to <20 g; and juveniles, <15 g) and color of pelage. Our observations of the species in Colima and elsewhere suggest that in juveniles and subadults the face tended to be grayish with yellowish coloration between eyes, while in adults the face often was more yellowish throughout; in juveniles and subadults, the black eye ring tended to be roundish in shape while adults had black that extended somewhat more toward the nose. Typically, animals were tagged in both ears using uniquely numbered Monel No. 1 ear tags (National Band and Tag Company, Newport, Kentucky) and released at site of capture. For some animals in 2007, only a single ear tag was used.

Estimation of movement, abundance, and density

For each *T. canescens* captured more than once, we determined mean distance of its trapping locations from the centroid of those capture sites, a distance hereafter referred to as distance from centroid (note that for an animal caught twice or more, but always at the same location, the resulting distance was 0 m). This approach to assessing movement is related to the center-of-activity concept as initially described by Hayne (1949). We also calculated minimum distance moved between successive captures for each individual and averaged the resulting values.

The computer program MARK (White 2007; White and Burnham 1999) was used to estimate abundance (i.e., population size) of *T. canescens* on grids. Assuming a closed population during the study of a grid, relative proportions of marked and unmarked animals in successive samples were compared within the program to provide an estimate of abundance, with parameters modeled as functions of each other. Two parameters—p, probability of capture, and c, probability of recapture—were involved in estimating N, the abundance for a given grid. We employed two models using data from all grids where *T. canescens* was present, with model 1 designated as $p(t)=c(t)$ and model 2 as $p(.)=c(.)$. For both, the estimated values for all grids were constrained to being the same. In model 1, p and c were set to be the same, but could vary from night to night (t). In model 2, p and c were constrained to be the same and not to vary from night to night (designated by periods in parentheses). AIC_c values were employed when evaluating which was the best model.

To convert abundance values into densities, it was necessary to calculate effective grid size. The immediate area of the grid (8,100 m^2; 90×90 m) does not take into account the effective grid area outside the outer traps. To estimate area of this edge, we employed mean distance from centroid, with equal weight being given to all individuals caught more than once. The resulting distance from centroid was added to each side of the central portion of the grid, and we considered corners of the grid to be rounded with a radius equal to this mean distance from centroid. Using distance from centroid as reported in Results, effective area of a grid was estimated to be 1.494 ha, a value divided into abundance values from MARK to obtain estimates of density (number of individuals/ha).

Structure of vegetation

Following Schnell et al. (2008), we quantified vegetation structure and other environmental characteristics by evaluating 14 variables (Table 2). For 2004–2007 and 2010, measurements were made at points 1 m from each trapping station (2,500 points total). Percentage of ground cover was estimated (to nearest 5 %) for a 1-m square (first seven variables in Table 2). 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 mean calculated (variable 8). Canopy cover (i.e., percent canopy closed, variable 9) was estimated using a spherical densitometer (model C, Forest Densitometers, Bartlesville, Oklahoma), as was slope (variable 10) with a clinometer. Using a 7.5-m vertical pole marked at each decimeter, we determined number of decimeter intervals within which vegetation touched the pole; resulting values were 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 estimated to the nearest 0.5 m (variable 13). Distance to nearest tree (10-cm diameter at breast height or greater) was determined in each of the four quadrants (with edges being the cardinal directions) and the mean calculated (variable 14); distances 10 m or greater were recorded as 10 m.

In 2003, similar measures were taken, but at 25 points/ grid instead of 100. The 25 were spaced equally among trapping sites. With the resulting values for each variable, we estimated the variable for each trapping station using ordinary and point kriging in the computer program Surfer version 8 (Golden Software, Inc. 2002). Resulting values were then treated the same as those for the other years.

Logistic regression, nonparametric multiplicative regression, and other statistical techniques

Using stepwise logistic regression (Systat Software, Inc. 2009) to assess habitat selection, we evaluated the relationship between vegetation structure and other environmental characteristics at trapping stations where *T. canescens* was caught and not caught. The dependent variable was presence or absence (1 or 0) of *T. canescens*, with the 14 environmental measures used as potential independent variables.

Table 2 Mean±SD (range) of 14 environmental variables, contrasting trapping stations where *Tlacuatzin canescens* was captured and not captured during 2003–2007 and 2010 in Colima, Mexico

	Variable	Stations where *T. canescens*	
		Captured (*n*=117)	Not captured (*n*=2,883)
1	Percent woody plants	6.5±8.76 (0–54)	6.4±10.12 (0–95)
2	Percent forbs	8.0±15.72 (0–90)	8.7±14.24 (0–100)
3	Percent grasses	9.2±12.64 (0–60)	13.1±26.29 (0–100)
4	Percent litter***	50.2±22.82 (0–95)	40.3±25.80 (0–95)
5	Percent dead wood	10.2±9.15 (0–45)	11.8±13.54 (0–95)
6	Percent rocks	3.4±6.06 (0–35)	4.3±9.70 (0–90)
7	Percent bare ground	12.5±15.27 (0–75)	15.3±18.38 (0–90)
8	Mean no. hits at 1 m*	1.7±1.50 (0–7.25)	2.5±4.41 (0–52.5)
9	Percent canopy closed	72.2±30.69 (0–100)	69.9±34.72 (0–100)
10	Slope (°)	6.3±6.82 (0–29)	6.8±8.71 (0–53)
11	Total hits low	4.7±3.68 (0–20)	4.6±4.32 (0–25)
12	Total hits high	3.7±4.98 (0–32)	4.7±6.45 (0–50)
13	Maximum canopy height (m)**	5.6±2.63 (1–15.5)	7.4±6.10 (0–35)
14	Mean distance to nearest tree (m)*	5.0±2.45 (1–10)	5.6±2.74 (0.75–10)

$*P<0.05$; $**P<0.01$; $***P<0.001$—statistically significant differences (one-way ANOVA)

Significance to include or remove a variable was set at 0.05, with maximum number of steps set at 10. McFadden's ρ^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. 2009).

Nonparametric multiplicative regression (NPMR), as implemented in the program HyperNiche (version 2.19; McCune and Mefford 2009), also was employed to model habitat selection based on the 14 environmental variables; the technique evaluates 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 a given environmental variable could be linear, but responses in the form of normal or bimodal distributions also could be identified). NPMR does not produce an equation but optimizes fit of data without reference to a specific global model. Results are represented as response curves or 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. We conducted an exhaustive search for the best model, where combinations of variables and tolerances (i.e., the SDs used in the Gaussian smoothers) were evaluated. After assessing single variables, all combinations of two variables, three variables, etc., were appraised until no further improvement in fit was achieved. To evaluate model fit, we used $\log_{10} B$, which is null deviance minus residual deviance (i.e., deviance of a model with no predictors), with the result divided by 4.60517 (McCune 2011). After an exhaustive search, we selected the best models predicting likelihood of occurrence for variables taken one at a time, two at a time, etc., and compared these "best" models using log *B*. We set an improvement criterion at 5 %, meaning that a best model with an additional variable would be considered only if adding of a variable would increase log *B* by at least 5 %.

Other techniques and approaches

SigmaPlot version 12 (Systat Software, Inc. 2011) was used graphically to compare environmental variables for stations where *T. canescens* was captured and not captured. BIOMstat for Windows 3.3o (Rohlf and Slice 1999) was employed for a variety of univariate analyses including row-by-column ($R \times C$) and goodness-of-fit tests for analyses of frequencies and one-way ANOVAs in assessments of continuous variables.

In addition to grid studies, we have trapped mammals at numerous localities throughout Colima. The resulting specimens were the basis for a distribution map of the species in the state. These records were supplemented with other museum records and published accounts of *T. canescens* in Colima.

Results

Based on specimens from our studies and those collected by other investigators, *T. canescens* occurs throughout the state of Colima (Fig. 1; for list of localities, see Appendix).

During 6 years (2003–2007 and 2010) involving 48,000 trap-nights on grids, we captured 82 individuals a total of 126 times. Most were caught in elevated traps (108 captures, 85.7 %).

General demographic characteristics

Of *T. canescens* captured, 69.5 % were adults (Table 3). For statistical analysis, we combined the small sample for 2006 with that for 2007. No significant difference was detected among years in percentage of captures that were adults ($R \times C$ test, $G=1.67$, $df=4$, $P=0.796$).

Overall, 48.8 % of *T. canescens* captured were males (Table 3) We evaluated whether the sex ratio differed from 1:1 for each year individually (but combining 2006 and 2007) and for all years pooled. For individual years 2003 through 2007, no deviation from the 1:1 sex ratio could be demonstrated statistically (goodness-of-fit tests, $G=0.091$, 0.699, 0.505, and 0.034, respectively, $df=1$, all $P>0.100$); however, in 2010, there was a significant deviation ($P=0.046$) with more females than males. For all years pooled, there was no significant difference from the expected 1:1 ratio ($G=0.049$, $df=1$, $P=0.825$). No significant heterogeneity was demonstrable in the sex ratio among years ($G=0.524$, $df=4$, $P=0.914$).

While January was at the end of the breeding season for *T. canescens* in Colima, we were able to determine whether adult females had been reproductively active during the previous reproductive period. For 21 adult females, the number postlactating and number that had not been reproductively active during the previous period, respectively, were as follows: 2004, 2 and 1; 2005, 0 and 2; 2007 1 and 5; and 2010, 0 and 10. Thus, overall, 3 of 21 adult females (14.3 %) had been reproductively active. For 34 adult males for which position of testes was recorded, numbers with scrotal and abdominal testes, respectively, were: 2003, 5 and 0; 2004, 1 and 4; 2005, 4 and 0; 2007, 11 and 3; 2010, 6 and 0. For all years, 79.4 % of adult males had scrotal testes.

There was no significant difference in mass between adult males and females (one-way AVOVA; $F_{(1, 55)}=$ 0.901, $P=0.347$). Means and SDs were 27.46±6.60 g for males ($n=36$) and 25.46±9.21 g for females ($n=21$).

In terms of movements, average distance from centroid for males was 14.51±8.25 m ($n=20$; range, 5.0–35.5 m), while that for females was 16.47±8.74 m ($n=12$; range, 0.0–32.1 m). No significant difference was detected between sexes (one-way ANOVA, $F_{(1, 25)}=0.409$, $P=0.527$). Pooling data from males and females, mean distance from centroid was 15.24±8.35 m ($n=32$, range 0.0–35.5 m). Using the pooled mean value, the effective area of a grid for *T. canescens* was estimated to be 1.494 ha.

Average minimum distance moved between successive captures for males was 31.90±20.97 m ($n=20$; range, 10.0–90.0 m) while that for females was 35.36±22.75 m ($n=12$; range, 0.0–89.4 m). No significant difference between sexes was detected (one-way ANOVA, $F_{(1, 30)}=0.193$, $P=0.664$). Pooling data from males and females, average maximum distance moved between successive captures was 33.19±21.35 m ($n=32$; range, 0.0–90.0 m).

We captured 1–12 *T. canescens* on 24 of 30 grids (Table 4). Model 1 for estimating abundance (where probability of capture and recapture were the same, but could vary among nights) was judged to produce the best estimates based on AIC_c values (505.46 for model 1; 512.02 for model 2). Abundances on occupied grids varied from 1.00–15.16 individuals/grid (Table 4); these values translate to density estimates of 0.72–8.03 individuals/ha. The estimates of probabilities of capture or recapture in model 1 were as follows: nights 1, 0.224; 2, 0.224; 3, 0.260; 4, 0.211; 5, 0.284; 6, 0.378; 7, 0.260; and 8, 0.211.

Habitat selection and characteristics of trapping stations

Mean values and SDs for the 14 environmental variables for trapping stations where *T. canescens* was caught and not caught are summarized in Table 2 for all years combined. When comparing variables individually, the following four variables—percent litter, maximum canopy height, mean distance to nearest tree, and average hits at 1 m—exhibited

Table 3 Numbers of *Tlacuatzin canescens* that were adult, sub-adult, and juvenile, plus indication of percent that were adults and percent that were male

Year	Age[a]			Total	Percent adult	Percent male
	Adult	Subadult	Juvenile			
2003	6 (6, 0)	5 (0, 5)	0 (0, 0)	11 (6, 5)	54.5	54.5
2004	9 (6, 3)	2 (2, 0)	2 (0, 2)	13 (8, 5)	69.2	61.5
2005	6 (4, 2)	2 (1, 1)	0 (0, 0)	8 (5, 3)	75.0	62.5
2006	1 (1, 0)	1 (1, 0)	0 (0, 0)	2 (2, 0)	50.0	100.0
2007	19 (13, 6)	6 (0, 6)	2 (0, 2)	27 (13, 14)	70.4	48.1
2010	16 (6, 10)	4 (0, 4)	1 (0, 1)	21 (6, 15)	76.2	28.6
Total	57 (36, 21)	20 (4, 16)	5 (0, 5)	82 (40, 42)	69.5	48.8

[a] Total with numbers of males and females, respectively, in parentheses

Table 4 Number of individuals captured and estimate of abundance (*N*) and density for *Tlacuatzin canescens* on grids where species was present in Colima, Mexico

Grid no.	No. animals captured	*N*±SE (95% confidence interval)[a]	Density (no./ha)
2003 (coastal Colima)			
1	2	2.00	1.34
2	1	1.00	0.67
3	1	1.00	0.67
4	6	6.00±1.468 (5.12–13.18)	4.02
5	1	1.00	0.67
2004 (coastal Colima)			
1	1	1.00	0.67
2	3	3.37±1.138 (3.02–10.46)	2.01
3	3	3.37±1.138 (3.02–10.46)	2.01
4	4	4.68±1.311 (4.06–11.80)	2.68
5	2	2.00	1.34
2005 (coastal Colima)			
1	4	4.68±1.311 (4.06–11.80)	2.68
2	1	1.00	0.67
3	1	1.00	0.67
4	2	2.00	1.34
2006 (northern Colima)			
3	1	1.00	0.67
5	1	1.00	0.67
2007 (northern Colima)			
1	1	1.00	0.67
2	9	11.24±2.002 (9.50–19.06)	6.02
3	12	15.16±2.346 (12.86–23.58)	8.03
4	5	6.00±1.468 (5.12–13.18)	3.35
2010 (central Colima)			
1	2	2.00	1.34
3	8	9.93±1.879 (8.39–17.56)	5.35
4	4	4.68±1.311 (4.06–11.80)	2.68
5	7	8.62±1.750 (7.29–16.08)	4.69

Estimates of abundance based on model 1, where $p(t)=c(t)$, with probability of capture (*p*) and recapture (*c*) being equal for a given night (*t*) but allowed to vary among nights. In model, values of *p* and *q* constrained to be the same for all grids

[a] With one or two individuals caught, no abundance estimate was possible using program MARK, so minimum number known to be alive was used

statistically significant differences between stations where *T. canescens* was caught and not caught (Table 2). Percent litter at stations where *T. canescens* was captured was higher than at stations where it was not captured, maximum canopy height (in meters) was lower, mean distance to nearest tree (in meters) was lower, and average number of hits at 1 m was lower.

Habitat selection evaluated using logistic regression and NPMR

Stepwise logistic regression of the 3,000 trapping stations on 30 grids, contrasting where *T. canescens* was caught and not caught, resulted in the equation

$$logit(Y) = -1.916 + 0.015X_4 - 0.168X_{13} - 0.174X_{14}$$

where logit (*Y*) is the natural logarithm of the odds of the species being present (which initially was coded as 1 when the species was caught at a station and 0 when not caught), X_4 is percent litter, X_{13} is maximum canopy height (in meters), and X_{14} is average distance to nearest tree (in meters). The resulting values of logit (*Y*) for stations where we captured *T. canescens*, in general, were higher than those for where the species was not encountered (Fig. 2a). McFadden's ρ^2 was 0.056. The *P* values for the constant and each coefficient were all <0.001. The SEs for the constant and coefficients were 0.391, 0.004, 0.033, and 0.040, respectively. The coefficient for percent litter was positive, indicating that *T. canescens* preferred locations with more litter (Fig. 2b). Coefficients for maximum canopy height and average distance to nearest tree were negative, indicating that locations where *T. canescens* was captured tended to have lower values for these variables than stations where it was not caught (Fig. 2c, d).

In total, 9,562 possible models evaluating up to five variables simultaneously were created using NPMR. The best one-variable model included percent grass, with models having two to five variables adding, sequentially, percent litter, maximum canopy height, percent canopy closed, and percent forbs (Table 5). The four-variable model was considered to be the best overall, given that adding another variable failed to improve log *B*, the measure of model fit, by 5 %.

In the four-variable model, the first variable—percent grass—had a curve for likelihood of occurrence of *T. canescens* that was hump-backed in shape, with likelihood of the species being present peaking when percent grass was about 30 % (Fig. 3a). There was little likelihood of finding *T. canescens* where percent grass was higher than 70 %. For percent litter, likelihood of the species being present was very low when there was no litter, with likelihood increasing gradually to about 0.05 at 60 % litter and tailing off slightly to 95 % litter (Fig. 3b). Data were insufficient to evaluate likelihood of occurrence for percent litter above 95 % (Fig. 3b); however, it is highly improbable that *T. canescens* would occur in such an area, even if it existed. *T. canescens* was more likely to be present when maximum canopy height was <10 m (Fig. 3c), with likelihood decreasing linearly to about 25 m and then to near zero at 33.5 m, the highest canopy we evaluated. The final variable included, percent canopy closed, also exhibited a hump-backed

Fig. 2 Percentages of trapping stations where *T. canescens* was caught and not caught in 2003–2007 and 2010. Percentages for: **a** projections of trapping stations in given classes for logistic-regression model where logit *Y* is natural logarithm of odds of species being present, X_4 is percent litter, X_{13} is maximum canopy height, and X_{14} is average distance to nearest tree; **b** percent litter; **c** maximum canopy height; and **d** average distance to nearest tree
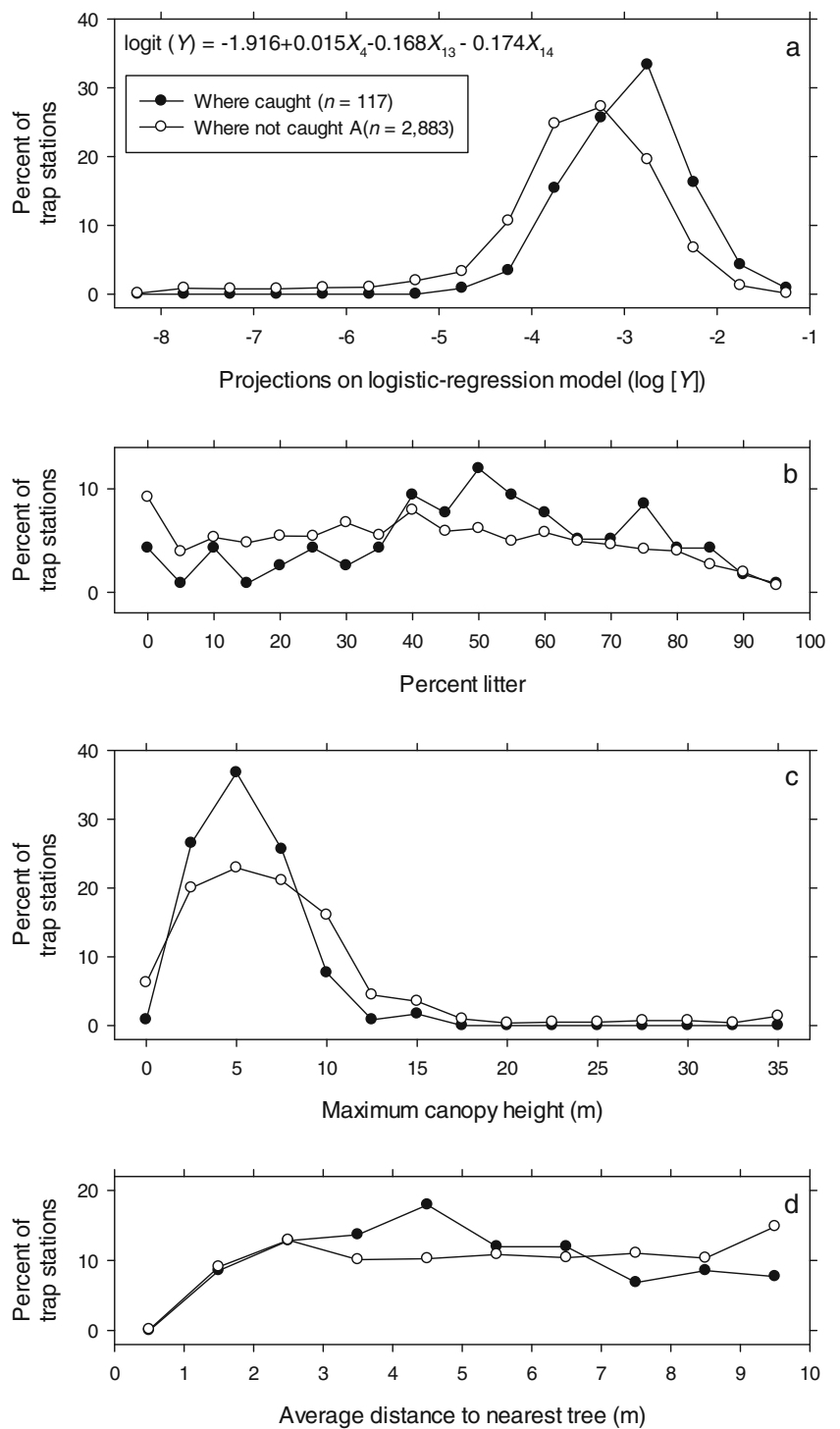
function, with the highest likelihood of occurrence being when the canopy was 30–50 % closed (Fig. 3d). The differences in likelihood were relatively slight over the whole range of canopy-closed values, which is why it was necessary to use a different vertical scale in Fig. 3d than in other panels of the figure; nevertheless, the trend was consistent indicating that *T. canescens* showed selection for intermediate percentages of canopy closed. Overall, the best model suggests that *T. canescens* more likely will be present when percent grass is about 30 %, there is a considerable amount of litter, canopy height is short, and the canopy is about 40 % closed.

Table 5 Best NPMR models for one to five predictors used to estimate likelihood of occurrence of *Tlacuatzin canescens* based on data from 30 grids in Colima, Mexico, for 2003–2007 and 2010 (117 trapping stations where species was caught and 2,883 where it was not caught)

No. variables	Log B	Δlog B	Average neighborhood size[a]	Variable (tolerance[b])
1	8.842		1,506.2	Percent grass (5.00, 5.00, 5.00, 10.00, and 10.00)[c]
2	13.235	4.393	572.6	Percent litter (14.25, 14.25, 14.25, and 14.25)
3	15.586	2.351	374.5	Maximum canopy height (5.25, 5.25, and 5.25)
4[d]	16.486	0.901	359.7	Percent canopy closed (40.00 and 45.00)
5	16.817	0.330	345.2	Percent forbs (40.00)

In this case, models with a higher number of variables include variables in models with fewer variables (although it is possible that variables in best models with higher numbers of variables are not inclusive of variables in best models with lower numbers of variables)

[a] Neighborhood size refers to stations nearby in multidimensional "environmental" space, with space defined by tolerances of variables in model

[b] Tolerance refers to SD of Gaussian weighting function that controls how quickly weights diminish with distance from 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 model. In local-mean models, tolerance inversely related to importance of variable in model (McCune 2011)

[c] Tolerance listed for this model and then, sequentially, for best models with higher number of variables

[d] Four-variable model judged best overall given log B of five-variable model did not meet 5 % improvement criterion

Discussion

Zarza et al. (2003) described *T. canescens* as being solitary, semiarboreal, and nocturnal, noting that 55 % of captures near Chamela in Jalisco were made on the ground (Ceballos 1990; Ceballos Gonzalez 1989). However, for the studies reported by Ceballos (1990) and Ceballos Gonzalez (1989), which covered all times of year, only 20 % of traps were in elevated positions; correcting for this differential, adjusted values indicate that *T. canescens* spent 76.6 % of time arboreally. Certainly, in January in Colima, *T. canescens* would be categorized as arboreal given that it was captured 85.7 % of the time in elevated traps during our study. Their arboreal activities involve nesting, with a number of nests having been located in tree and cactus hollows, as well as abandoned hanging nests of birds (Armstrong and Jones 1971; Gaviño de la Torre and Vargas Yañez 1993; Sánchez-Hernández and Romero Almaraz 1995; Zarza et al. 2003). An omnivore, *T. canescens* appears regularly to feed in arboreal situations; it has been found in hanging and elevated bird nests, likely having eaten eggs (Sánchez Hernández and Gaviño de la Torre 1988), and is thought to search out insects and other prey in trees. It also has been recorded feeding on nectar and probably associated insects (beetles and ants) in flowers of the cactus *Stenocereus queretaroensis* (Ibarra-Cerdeña et al. 2007).

Two other small marsupials—*Marmosa robinsoni* and *M. mexicana*—occur in Mexico and Central America (O'Connell 1983; Alonso-Mejía and Medellín 1992), with the latter having a geographic distribution that in part overlaps with that of *T. canescens*. Ceballos and Oliva (2005) indicated that *M. mexicana* is totally arboreal while *T. canescens* is semiarboreal, although as indicated above, data for *T. canescens* indicates it is highly arboreal as well. *M.*

robinsoni appears to frequent the ground more readily than do the other two species (O'Connell 1983). Both *M. mexicana* and *T. canescens* are found in a variety of habitats, including cultivated cropland and disturbed areas, while O'Connell (1983) noted that information from several studies suggests that *M. robinsoni* prefers secondary forest and disturbed farmlands to undisturbed habitats.

General demography

Over the 6 years of our January studies, 3 of 11 adult females (27.3 %) were postlactating. Several authors have indicated that *T. canescens* generally breeds in summer but can breed year-round (Armstrong and Jones 1971; Ceballos 1990; Zarza et al. 2003). Armstrong and Jones (1971) reported two females with embryos or young in September and another in October that was lactating, while Ceballos (1990) noted females with young in July through September. Our findings indicate indirectly that in Colima breeding sometimes occurs in December.

To date, no one has reported on sex ratio of this species. Our data suggest that the ratio of males to females does not deviate from 1:1. Likewise with body mass, there is no report regarding the degree, if any, of sexual dimorphism in this physical characteristic. Although the males we captured tended to be heavier than the females, we detected no statistical evidence of a difference in average mass between males and females.

Movements of males and females between captures were about the same. Ceballos Gonzalez (1989) conducted a mark-and-recapture study near Chamela in Jalisco and reported an average distance between successive captures for *T. canescens* of 35.2 m, which is similar to our mean value of 33.2 m. For *M. robinsoni* in the Panama Canal

Fig. 3 Likelihood of occurrence of *T. canescens* relative to **a** percent grass, **b** percent litter, **c** maximum canopy height (in meters), and **d** percent canopy closed for best NPMR model overall, which had four variables. Based on data from 30 grids in Colima for 2003–2007 and 2010 (3,000 trap stations; 117 where *T. canescens* was caught and 2,883 where the species was not caught). Vertical scale in (**d**) expanded relative to other panels
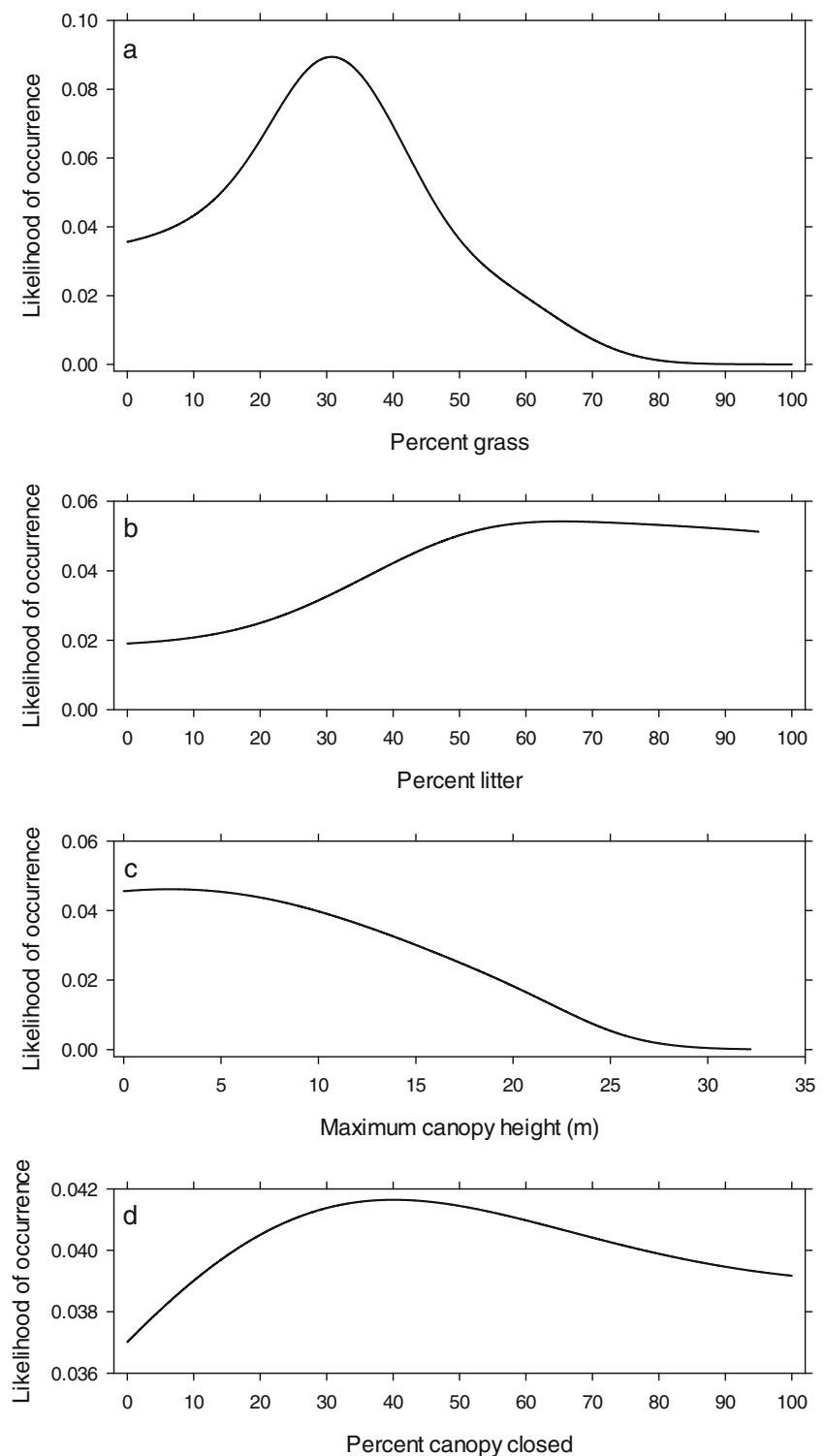
Zone, average distances between successive captures were somewhat higher, being 58.5 m for males and 46.6 m for females, although the interspecific difference was not significant statistically.

Ceballos (1990) estimated population densities of *T. canescens* near Chamela based on minimum number known to be alive. In deciduous and arroyo forests of his study, density was 0.4–4.5 individuals/ha during April 1986–June 1987. Most of our sites were relatively undisturbed, and densities ranged from 0.67–8.03 individuals/ha, the latter being substantially higher than recorded by Ceballos (1990). Fleming (1972) reported minimum densities estimates for *M. robinsoni* in the Panama Canal Zone of 0.31–2.25/ha, which are values typical of densities we

encountered for *T. canescens* on many of the grids but are lower than we found on relatively high-density sites. In northern Venezuela, density of *M. robinsoni* ranged from 0.25–4.25/ha (O'Connell 1979).

A question arises as to whether the use only of oats as bait may have resulted in fewer captures and lower density estimates than would have been the case if a bait mixture had been used. For example, Ceballos (1990) baited traps with a mixture of rolled oats, peanut butter, and vanilla extract, while López-Forment et al. (1971) used crushed oats and coconut. No one has conducted a comparative study at a given locality of the efficacy of different baits in attracting *T. canescens*. However, given that density estimates from our study in general were higher than those emanating from the study by Ceballos (1990), there is no evidence at present that the bait we used resulted in reduced capture rates. Furthermore, in our extensive fieldwork (off grids) in Colima, we have on occasion used other baits (e.g., mixtures of peanut butter and rolled oats, rolled oats and banana, banana and peanut butter). Captures did not exceed those when we used rolled oats alone, and there was no evidence to suggest that other baits were better than rolled oats. Densities of *T. canescens* tend to be low at most sites, although higher in several locations than recorded, for example, for another small marsupial, *M. robinsoni*, in the Panama Canal Zone and in northern Venezuela (Fleming 1972; O'Connell 1979).

Ecological characteristics and comparison of methods for evaluating habitat selection

T. canescens has been reported to occur in semideciduous forests and secondary vegetation (Hernández-Cardona et al. 2007; Loomis and Stephens 1962; Sánchez-Hernández et al. 2009; Vargas-Contreras et al. 2004; Villa-Ramírez 1991; Zarza et al. 2003). We found the species in both. One most likely would encounter the species at locations with considerable litter. While we captured *T. canescens* in forests with a range of characteristics, the species was most frequently recorded when height of forest canopy was low. Ground cover of about 30 % grass was preferred by the species, with it being less likely to be present if there was a higher or lower percentage. In addition, *T. canescens* showed selection for sites where the canopy was relatively open (i.e., 30–50 % closed).

We employed univariate comparisons, logistic regression, and NPMR to assist in elucidating habitat selection of *T. canescens*. It is legitimate to question whether there is value in application of multiple approaches when analyzing a data set. It also is of interest to determine whether the different approaches resulted in different conclusions and, if so, why. Our study of habitat selection of *T. canescens* did produce different but related answers based on the different approaches to data analysis. Univariate ANOVAs identified

significant differences between stations where the species was caught and not caught for four variables (percent litter, mean number of hits at 1 m, and maximum canopy height, and mean distance to nearest tree). Logistic regression produced an equation that included three of these variables, leaving out only mean number of hits at 1 m because it did not add substantially to differentiation between capture and noncapture sites when taken in combination with the other three variables. Overall, results from univariate tests and logistic regression largely agreed.

In the best model produced using NPMR, two variables (percent litter and maximum canopy height) were included that had been deemed important by ANOVA and logistic regression for differentiating capture and noncapture sites. In addition, NPMR incorporated two variables (percent grass and percent canopy closed) that were not identified as useful for contrasting capture and noncapture sites by either univariate ANOVAs or logistic regression. In fact, percent grass provided the best differentiation of any of the variables in the NPMR model with only a single variable (first row in Table 5).

Both percent grass and percent canopy closed exhibited hump-backed distributions in likelihoods of occurrence (Fig. 3a, c), which explains why they were not highlighted by ANOVA or logistic regression but were given consideration by NPMR. McCune (2011) pointed out that default response shapes being evaluated by statistical techniques as typically applied are linear (such as with multiple regression) or sigmoidal (e.g., logistic regression). With one-way ANOVA, one is evaluating variances and looking for differences in means. The standard theoretical concept for relationship of a species to an environmental gradient is a unimodal, hump-shaped curve (McCune 2011); however, a curve of this shape, if present, would not be detected by ANOVA or logistic regression. NPMR, however, recognizes a response curve of this form and, in the case of percent grass and percent canopy closed, indicated that *T. canescens* has a decided preference for intermediate values on these environmental gradients given the range of values represented in Colima. Habitat modeling with NPMR not only considers a wide range of potential response curves by a species, but can do this in multiple dimensions (multiple predictor environmental variables) while also taking into account potentially complex interactions among those variables. NPMR has provided us with insight into habitat selection of *T. canescens* not revealed by other techniques.

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Appendix

Gazetteer of localities in Colima, Mexico, where *T. canescens* has been captured. Locality numbers (in parentheses) refer to those in Fig. 1. In two cases, geographically close localities are represented by a single symbol on map (herein, for these locality pairs, lowercase letters have been added to locality number). Localities ordered by municipality (in bold). Latitude and longitude in decimal degrees included in brackets. Records include those from specimens we have collected and other specimens in the following collections: American Museum of Natural History; Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México; Instituto Politécnico National; National Museum of Natural History, Smithsonian Institution; Natural History Museum and Biodiversity Research Center, University of Kansas; Natural History Museum of Los Angeles County; and Sam Noble Oklahoma Museum of Natural History, University of Oklahoma.

Manzanillo: (1) El Centinela, 3 miles (4.8 km) S El Chavarín, 3 miles (4.8 km) E Colima/Jalisco border (19.1758140° N, 104.5914487° W); (2) El Charco (19.2439085° N, 104.4945587° W), 50 ft (15 m); (3) Playa de Oro, 19°08.100′ N, 104°29.957′ W (19.1350000° N, 104.4993000° W); (4) La Huiscolotila (19.2211967° N, 104.3783889° W); (5) Camotlán (19.2195390° N, 104.235314° W); (6) Agua Blanca, 19°03.961′ N, 104°03.152′ W (19.0660200° N, 104.0525000° W), 141 m. **Minatitlán:** (7) 1 km NW Ranchitos (19.4119396° N, 103.9690770° W), 1,550 m. **Comala:** (8) 10 miles (16.1 km) NW Comala, 1,980 m (19.4094366° N, 103.8798590° W); (9) Comala (19.3320930° N, 103.7552980° W). **Villa de Álvarez:** (10) Mixcuate (Miscuate; 19.3161590° N, 103.9346275° W). **Coquimatlán:** (11) El Algodonal, NW de Agua Zarca (ca. 19.2585916° N, 103.9789445° W); (12) Pueblo Juárez, 6 km N Agua Zarca (19.2614437° N, 103.9397589° W). (13) 9 km W Pueblo Juárez (19.1670250° N, 104.0172530° W; incorrectly designated as in municipality Villa de Álvarez); (14a) Pueblo Juárez (19.1674296°N, 103.9314468° W); (14b) hacienda La Magdalena above 1,500 ft (330 m); (15) 3 km ESE Pueblo Juárez, 19°09.867′ N, 103°55.069′ W (19.1644500° N, 103.9178000° W), 240 m; (16) El Paraiso, 1 km W Río Armería, 19°08.76′ N, 103°51.9′ W (19.1460000° N, 103.8650000° W), 220 m. **Tecomán:** (17) 5 km NE Tecolapa (19.0546667° N, 103.7833333° W). **Armería:** (18) on highway 110 at east side of bridge over Río Armería, 3.2 km E Armería (18.9344592° N, 103.9402019° W). **Cuauhtémoc:** (19) 4.5 km E Palmillas, 19°21.25′ N, 103°30.44′ W (19.3505511°N, 103.5134912°W), 805 m. **Colima:** (20) Cuauhtémoc, 6 km S Cuauhtémoc, Miguel de la Madrid Airport, 710 m, 19°16.083′ N, 103°36.000′ W (19.2680500° N, 103.6000000° W); (21) 15 km SE Colima (19.1263380° N, 103.6299681° W); (22) 1.5 km S, 3.0 km E Los Asmoles, 19.1044700° N, 103.7472000° W, 350 m; (23) 18 km SE ciudad de Colima (19.0942364° N, 103.6178522° W). **Ixtlahuacán:** (24) 1.6 km NE Las Conchas, 18°53.50′ N, 103°38.721′ W (sic; 18.8974644° N, 103.6205008° W), 30 m.

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