Waxing and Waning of a Cotton Rat (Sigmodon toltecus) Monoculture in Early Tropical Restoration

Authors: Howe, Henry F., and Davlantes, Jason

Waxing and Waning of a Cotton Rat (*Sigmodon toltecus*) Monoculture in Early Tropical Restoration

Henry F. Howe[1] and Jason Davlantes[1]

Abstract

As part of an experimental restoration of seed-dispersal processes in a fragmented agricultural landscape, we recorded rodent colonization of fenced plots in active cattle pasture over 10 years. The design included 16,900 m^2 fenced cattle exclosures that were either planted with seedlings of native animal-dispersed trees, planted with seedlings of native wind-dispersed trees, or unplanted controls to simulate natural succession. Near the end of the dry season in late May and early June from 2007 to 2016, five Sherman live traps were placed in each plot for 66 hr per plot, resulting in 1,584 trap hours per year. Eight species of rodents were captured. Of 697 individuals, 644 (92%) were cotton rats (*Sigmodon toltecus*); only 1 other species, Coues' rice rat (*Oryzomys couesi*), accounted for >1% of the total. *S. toltecus* accounted for at least 96% of the biomass of >50 kg of rodents captured. This species dominated the rodent community while most plots were grass- or fern-covered from 2007 to 2010. Thereafter, the question of interest was whether *S. toltecus* change in population numbers could be attributed to normal fluctuations of small rodents or to habitat change. The minimum number alive declined from 149 in 2010 to 20 in 2016. Overall, and frequently within years, low *S. toltecus* captures reflected high woody cover from shrubs and trees. A virtual *Sigmodon* monoculture prevailed until dense herbaceous cover was replaced by forest understory.

Keywords

experimental restoration, habitat use, Los Tuxtlas, Mexico, rodents, tropical ecology

Introduction

Agricultural landscapes bordering forest in the Los Tuxtlas Biosphere Reserve are mosaics of pastures, orchards, isolated trees, lines of living fences, and forest fragments (Guevara, Laborde, & Sánchez-Ríos, 2004). The landscape retains substantial plant diversity (Arroyo-Rodríguez et al., 2013) and, given the intensity of agricultural development, surprising mammalian diversity (Estrada, Coates-Estrada, & Merrit, 1994; Flores, Coates, Sánchez-Cordero, & Mendieta, 2014). Overgrazed pastures are species-poor, with a preponderance of alien grasses cropped to 5 to 10 cm from the ground, and very few native terrestrial mammals. Mammalian presence in early succession of land released from pasture or in early stages of ecological restoration is not well documented. This is of interest because in the Temperate Zone, small rodents can dramatically alter communities of herbaceous prairie vegetation (Howe, Sullivan, Zorn-Arnold, & Brown, 2006) and even change the course of oldfield succession back to forest

(Ostfeld, Manson, & Canham, 1997). Here, we report small-rodent presence in the first 10 years of rodent succession, dominated by the cotton rat *Sigmodon toltecus*, in fenced plots embedded in active cattle pasture adjacent to the Los Tuxtlas Biosphere Reserve.

The ecology of *S. toltecus* is not well known compared with its ecologically diverse congener, *S. hispidus*. *S. toltecus* occurs in forest and citrus orchards in southern Mexico but is most common in pastures or in forest fragments, in the latter probably coincident with pasture edges (Estrada et al., 1994; San-José, Arroyo-Rodríguez, & Sánchez-Cordero, 2014). Presence of this species in numbers could be important: In the Temperate Zone,

[1]Department of Biological Sciences, University of Illinois at Chicago, IL, USA

Corresponding Author:
Henry F. Howe, Department of Biological Sciences, University of Illinois at Chicago, Chicago, IL 60612, USA.
Email: hfhowe@uic.edu

selective granivory and herbivory by smaller rodents (*Microtus ochrogaster* or *M. pennsylvanicus*) can dramatically influence species composition of herbaceous prairie vegetation or even change the path of forest succession (Howe et al., 2006; Ostfeld et al., 1997). While this is not an exclosure experiment that could definitely test the role of pasture rodents in succession, it is of interest to determine which species occupy early restoration.

In the interest of developing habitat heterogeneity that restores seed-dispersal processes in biodiversity-friendly landscapes (Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013), we track rodent occupation of 24 experimental restoration plots (*sensu* Howe & Martinez-Garza, 2014) in southern Mexico. Questions of interest include the following: (a) Which rodents occupy successional stages of fenced plots changing from closely grazed pasture to small forest patches? (b) Are changes in rodent species associated with cover of woody vegetation or population fluctuations for other reasons? Because the dominant rodent turned out to be the little-studied cryptic species *S. toltecus*, this study offers ecological insight into the ecology of this genetically defined species.

Methods

Species and Nomenclature

This study contributes to a sparse ecological literature on a genetically differentiated cryptic species, *S. toltecus*, about which far less is known than its congeners north of Mexico. *Sigmodon hispidus* (Cricetidae) was long considered a single species with a geographical range from eastern and central North America to South America. Analyses of sequences of mitochondrial cyctochrome *b* DNA and a nuclear fibrinogen gene show sufficient genetic divergence to divide a species complex into three major clades (Peppers, Carroll, & Bradley, 2002). One, the *hispidus* clade, represents up to seven cryptic species, with three clearly defined genetic species—*S. hispidus*, *S. hirsutus*, and *S. toltecus* (Carroll, & Bradley, 2005). *S. toltecus* is a mostly coastal rodent from lowlands of northern Tamaulipas to Belize and coastal Honduras (Bradley, Henson, & Durish, 2008). The species resembles *S. hispidus* externally (Engilis, Cole, & Caro, 2012). Species status reflects average genetic distances of 12.81% in mitochondrial cytochrome *b* DNA between *S. toltecus* and *S. hispidus*, sympatric in northeastern Mexico, and 12.90% difference with mostly higher elevation *S. hirsutus*, geographically sympatric in Chiapas, Mexico. The "*hispidus* clade" differs from congeneric clades by 17% to 20% in cytochrome *b* and up to 5% in nuclear genes tested. Phylogeographies of other rodent genera are likely to show cryptic genetic speciation throughout Mesoamerica and South America

(Baker & Bradley, 2006), representing widespread challenges to biodiversity conservation, including genetic diversity.

Nomenclature for birds follows the American Ornithologist Union (2016), for mammals, other than *S. toltecus*, Wilson and Reeder (2005). Plant nomenclature follows *Tropicos* of the Missouri Botanical Garden (2016).

Study Site

The study site is a set of 24 fenced plots in 12 ha of heavily grazed pasture embedded within a landscape of adjacent pasture, forest, scattered tree stands, and isolated individual trees 182 to 260 m above sea level (central GPS point 18° 35.732′ N, 95° 06.109′ W). The landscape is of volcanic origin, with soils absent over exposed rocks to >1.5 m deep overlying volcanic rubble (see Garcia-Aguirre, Alvarez, Dirzo, Ortíz, & Eng, 2010). Once covered with lowland rainforest, the region is largely deforested with the exception of remnants in the Los Tuxtlas Biosphere Reserve (Arroyo-Rodríguez et al., 2013). Precipitation varies from 2.7 m in a drought year to a mean of 4.8 m in normal years (Martínez-Garza, Tobon, Campo, & Howe, 2013).

Restoration plots embedded in active pasture impose predation risk on young and adult rodents. Many predators occur in nearby forests. Aerial predators observed at the site by authors and project personnel include barn owl (*Tyto alba*), white hawk (*Leucopternis albicollis*), common black hawk (*Buteogallus anthracinus*), roadside hawk (*Buteo magnirostris*), short-tailed hawk (*Buteo brachyurus*), crested caracara (*Caracara plancus*), migrant American kestrel (*Falco sparverius*), and Aplomado falcon (*Falco femoralis*). Terrestrial predators observed at the site include *Boa constrictor*, coyote (*Canis latrans*), opossums (*Didelphis marsupialis* and *D. virginiana*), and coati (*Nasua narica*). Of these, the greatest local threats to small rodents in the first 10 years are probably *T. alba*, *B. anthracinus*, *B. constrictor*, and of young rodents *D. marsupialis* and *D. virginianus*.

Site Layout

Experimental restoration began in 2006 with the establishment of 24 fenced and planted or control 30 × 30 m plots in active cattle pasture. In September and October 2006, eight plots were planted with seedlings of 12 individuals of each of 12 species of native animal-dispersed trees, eight with 12 individuals of each of 12 species of native wind-dispersed trees or were fenced and unplanted to simulate natural succession (Martínez-Garza et al., 2013). Seedlings of 18 species that successfully germinated and grew in a shade house were 4 to 7 months old when planted at a median height of 16 cm. Plots were spaced

30 m apart. Plots were 100 to 415 m from privately owned secondary and old-growth forests, which were continuous with forest of the Los Tuxtlas Biological Station (640 ha) and the eastern end of the Los Tuxtlas Biosphere Reserve (Volcán San Martin Tuxtla and surrounding forest; total area of the Biosphere Reserve is ~155,000 ha). Exceptional dry season drought killed most seedlings between April and July 2007; plots were replanted with some species substitution from August to October 2007.

Woody cover was negligible 2006 to 2008, but vegetation matured to a median of 85% woody cover in 2016. By 2016, most solely herbaceous cover was in control plots (Figure 1). Vegetation was sparse and brown in pastures and exclosures during the 2007 drought; regrowth from August 2007 through early 2009 was of sparse to thick grasses of mostly exotic origin (e.g., *Cynodon dactylon*, *C. plectostachyus*, *Brachiaria brizantha*, *B. decumbens*, and *Panicum* spp.) and the invasive fern *Nephrolepis hirsutula*, all reaching a canopy cover of 0.5 to 1.3 m, depending on soil depth and species. Woody cover of planted trees and recruited shrubs and trees that were not planted began to cast sufficient shade to suppress grasses and ferns in scattered locations in 2009. Crown area and shade from woody vegetation developed most rapidly from wind-dispersed pioneers in stands of planted wind-dispersed trees (Martínez-Garza, Bongers, & Poorter, 2013). Beginning in June 2009, woody cover was estimated annually for each plot to the nearest 5% of plot area.

Sampling Rodents

Small rodents were captured and released in late May or early June in each plot over 3 nights, 2 full days, and part of 2 days from 2007 to 2016. Five Sherman traps (7.62 × 8.89 × 22.86 cm) were placed on the ground in each plot, totaling 66 trap hours per 30 × 30 m plot per year. Bait was approximately 8 g of sunflower seeds and oatmeal in equal proportion by volume inside and at the mouth of each trap. Total trap hours were 1,584 per year and 15,840 over 10 years. Traps were checked in morning and late afternoon 2006 to 2013 and rebaited and reset when necessary (e.g., after a capture), necessitated by 10 to 20 captures the first morning. Subsequently when the first trap day yielded 0 to 4 captures, traps were checked in the morning. Each animal was identified to species, sexed and weighed to the nearest 0.1 g. Pregnant and lactating females were noted. A 1 cm^2 patch of fur was cut to identify recaptures and allow estimation of the minimum number alive. Resources limited sampling to one first-author trip per year; similar constraints made resampling and permanent markings feasible. The Los Tuxtlas Biological Station retained vouchers from the area.

When an animal of sex, body mass, and clipping pattern was recaptured in a plot where no individual with similar attributes had been captured, the best match was sought in other plots. The procedure was to match size, sex, and clipping patterns with recaptures in the closest neighboring plot as measured by the distance from the center of the initial capture plot to the middle of the nearest likely recapture plot. This is conservative in that an animal might move further than the nearest plot and may overestimate movement in that distance estimates were between plot centers.

Analyses

Statistical analyses were performed in Systat 13 and R. Plots planted with animal- and wind-dispersed trees were indistinguishable in cover and occupation by *S. toltecus*. Analyses were pooled as "planted" versus "control" treatments because no differences were noted in rodent response variables of planted animal-dispersed or
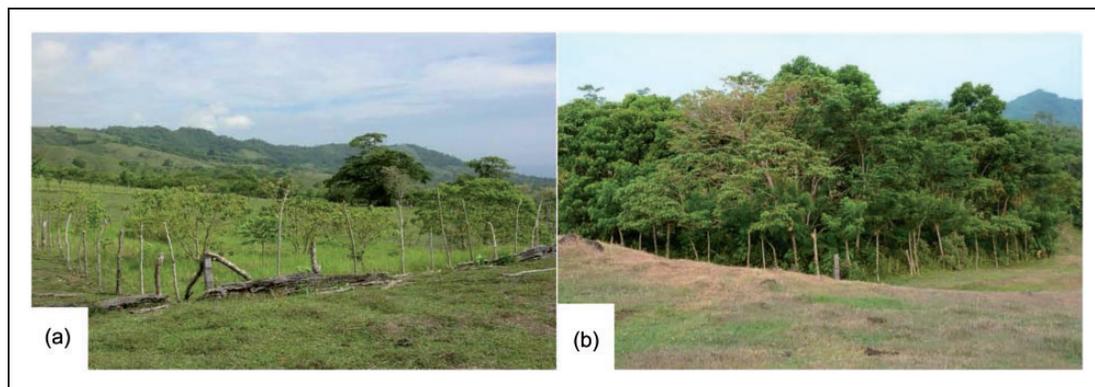

Figure 1. A plot of wind-dispersed trees. (a) A typical planted plot in 2009: only occasionally did young trees cast enough shade to suppress grasses. (b) The same plot from a different angle in 2016; grasses in planted plots were gone, although some plots had undergrowth of ferns or juvenile angiosperms.

wind-dispersed stands. Means are accompanied by standard errors.

Results

Overview

The number of *S. toltecus* trapped per plot ranged from 0 to 12. *S. toltecus* was far the most-trapped species (overall 92%), even from 2014 to 2016 when it averaged one or fewer individuals per plot (Table 1). Because *S. toltecus* were heavier than most other trapped species, summed body mass also reflected higher biomass than other species (~96%; Table 2). Using an adult-juvenile cutoff of 50 g (Bergstrom & Rose, 2004), 430 adult *S. toltecus* averaged 92.6 ± 1.0 g *SE*, with 222 females averaging 90.3 ± 1.2 g and 208 males averaging 95.1 ± 1.5 g ($t = -2.538$, df $= 428$, $p = .012$). Seventy females (32%) that were lactating or pregnant averaged 96.0 ± 2.0 g, while 151 adult females that were not reproductive

averaged 86.6 ± 1.5 g ($t = -3.794$, df $= 220$, $p < .0001$). Of the 593 *S. toltecus* with measured body weight, 101 (17%) were immature (<50 g). The smallest reproductive females were 58 g, 60 g, and two at 62 g. Overall, the summed body masses of 44,637 g were recorded in this project (Table 2). If mean body mass were used to estimate summed weights in 2011, when accurate body masses were not available (61×81 g $= 4,965$ g), the summed mass of all *S. toltecus* would exceed 50 kg.

Capture and recapture rates varied for *S. toltecus*. The normal pattern was low capture the first night that 60 traps were set in each half of the plots, more in the next two nights. Four times as many animals were caught overnight as during the day. Of 430 adult *S. toltecus* sexed and weighed, 113 (26%) were recaptured at least once, with some individuals recaptured three to five times. There was no sex bias in recaptures. An ANOVA testing for differences in body mass by sex, recapture or not, and their interaction found that adult males were 5 g heavier than adult females, $F(1, 426) = 7.478$, $p = .007$; recaptured

Table 1. Minimum Number of Small Rodents Alive in 24 30 × 30 m Restoration Plots Near the Los Tuxtlas Biological Station, Mexico, Over 10 Years.

Species	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Oligoryzomys fulvescens	0	0	1	0	0	2	0	0	1	2
Oryzomys alfaroi	0	0	0	1	0	0	0	0	2	3
Oryzomys couesi	0	1	0	0	0	5	5	0	5	1
Oryzomys rostratus	0	0	0	0	0	0	0	0	0	1
Peromyscus Mexicanus	0	0	0	0	0	2	1	0	1	0
Reithrodontomys fulvescens	0	1	1	2	0	0	0	0	1	1
Sigmodon toltecus	1	71	149	133	61	100	56	28	25	20
Tylomys nudicadatus	0	0	0	0	0	0	0	1	0	0
Total	1	73	151	136	61	114	61	29	33	28
S. toltecus (%)	100	97	99	98	100	91	90	97	70	71

Table 2. Biomass of Rodents for Which Weights Were Available in Restoration Plots 2007 to 2016.[a]

Species	*N*	*M* ± *SE* (g)	Mass species[a] (g)	%
Oligoryzomys fulvescens	6	15.4 ± 1.1	92	0.2
Oryzomys alfaroi	6	39.3 ± 3.6	236	0.5
Oryzomys couesi	17	61.5 ± 2.6	1,046	2.2
Oryzomys rostratus	1	63.00	63	0.1
Peromyscus mexicanus	4	37.5 ± 2.8	150	0.3
Reithrodontomys fulvescens	6	10.3 ± 1.5	62	0.1
Sigmodon toltecus	548	81.4 ± 1.4	44,637	96.0
Tylomys nudicaudus	1	223.0	223	0.5

[a]Excluding 2011.

adults $(95.7 \pm 1.7\,\mathrm{g})$ were slightly heavier than those not recaptured $(91.5 \pm 1.1\,\mathrm{g}$; $F(1, 426) = 4.128$, $p = .043)$. Some capture rates were extremely high. In 2010 and 2012, 43% and 44% of the animals were recaptured at least once. In the penultimate night of trapping in 2010, 49 of 60 traps (82%) held captures, of which 18 (37%) were recaptures. In the final night of trapping that year, 45 of 60 traps (75%) had captures, of which 22 (49%) were recaptures. These capture rates contrasted with 2014 to 2016 censuses, when overall trap success was <7% per night and sometimes 0% per night.

After the penultimate night of trapping in 2010, 49 of 60 traps (82%) held captures, of which 18 (37%) were recaptures. In the final night of trapping in 2010, 45 of 60 traps (75%) had captures, of which 22 (49%) were recaptures. High capture rates contrasted with 2014 to 2016 censuses, when overall trap success was <7% per night.

Some recaptures occurred in plots other than the one in which an animal was first encountered. Five of 102 juveniles were recaptured in plots other than the one in which they were first caught. Three traveled at least 60 m, one 150 m, and one 39 g male 430 m. At least 20 adult females and 12 adult males were recaptured in plots other than the ones in which they were first caught. Of these, 15 adult females moved at least 60 m and 5 moved >130 m. Of adult males, seven moved at least 60 m and

five moved >130 m. In these samples, females moved more than males $(\chi^2 = 8.72$, df = 1, $p < .005)$.

Numbers by Habitat

The question of whether changes in minimum number of *S. toltecus* alive reflect ups and downs of population dynamics or habitat change is surprisingly difficult to tease apart (Figure 2). Excluding the one individual caught in the drought year 2007, when there was no woody cover and practically no grass cover up to 10 cm high at the site, the mean number of individual *S. toltecus* trapped per plot showed strong negative correlations with both mean woody forest cover per plot $(r = -0.71)$ and year $(r = -0.77)$, respectively (Figure 2). Mean woody cover of plots increased dramatically with time, with most planted plots fully shaded and control plots partially shaded by trees in 2016.

Minimum numbers of *S. toltecus* alive per plot and woody cover per plot changed dramatically from 2007 to 2016 (Figure 2). Data did not meet assumptions of a repeated-measures analysis of variance over most of the study period. An analog of repeated measures for non-independent samples over time, the Friedman non-parametric analysis of variance, showed that rankings of *S. toltecus* captures by plot changed substantially from 2008 to 2016 (Friedman Statistic 103.946, df = 8,
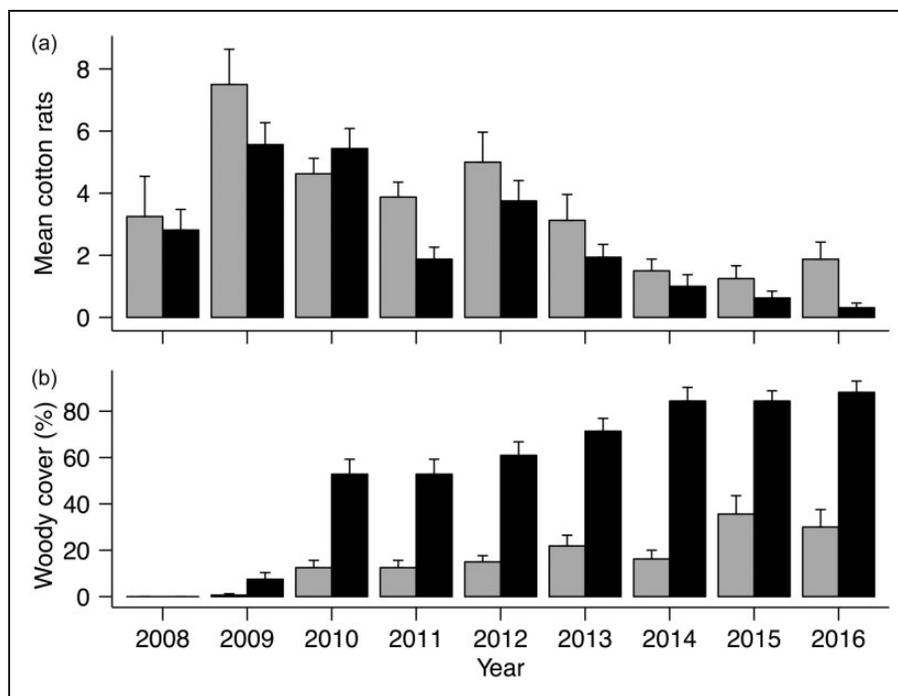

Figure 2. Changes in *Sigmodon toltecus* and woody tree cover by planting treatment. (a) Disparity in woody tree cover in planted plots (black) as compared with controls (gray) from 2008 to 2016. Indicated are estimates of m^2 of plots shaded by trees enough to suppress grasses out of 900 m^2 in each. (b) Increase and then decrease of minimum number of cotton rats (*S. toltecus*) per plot in planted (black) and control (gray) treatments. Shown are means and standard errors.

Table 3. Number of *S. toltecus* Captured by Treatment From 2008 to 2016.[1]

Treatment	2008	2009	2010	2011	2012	2013	2014	2015	2016
Animal-dispersed plots	19	46	46	14	39	16	5	6	2
Wind-dispersed plots	22	42	42	16	19	14	11	5	3
Control plots	26	50	40	31	39	26	10	11	15

[a]Excludes single capture in 2007. Rank order changed by treatment over 9 years (Friedman statistic 22.387, df = 8, p = .004).
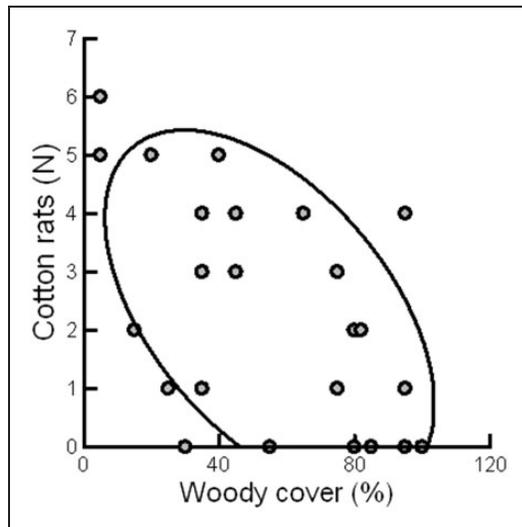

Figure 3. Negative relationship between *S. toltecus* and woody cover in 2013. Each dot is a plot. Ellipse is 68% ($r = -0.52$, p = .01).

$p < .001$; Table 1). A more direct test for changes in rank-order abundance by treatment was also significant (Friedman Statistic 22.387, df = 8, $p < .004$), with more animals trapped in control treatments than others in most years after 2010 (Table 3).

Change in minimum numbers of *S. toltecus* alive per plot and woody cover per plot with treatment (controls or planted; Figure 2) could be subjected to repeated measures between 2010 and 2012. The analysis showed changes in *S. toltecus* per plot by treatment, $F(1, 21) = 59.448$, $p < .001$, and a *S. toltecus* number by treatment interaction, $F(1, 21) = 21.364$, $p < .001$, over those 3 years. Woody cover also changed over time, $F(1, 21) = 8.834$, $p < .01$, and by treatment, $F(1, 21) = 5.289$, $p < .05$, with a *S. toltecus* by woody–cover interaction, $F(1, 22) = 9.486$, $p < .005$.

A potentially more informative approach tested correlations between the number of *S. toltecus* per plot trapped under woody versus herbaceous cover within a census year (Figure 3). Low woody cover early in the experiment and low rodent numbers later complicated this approach. Correlation was not possible in 2008 because there was no woody cover. In 2009, a negative Spearman correlation ($r_s = -0.544$, $p < .01$) was clearly due to extreme values (some plots lacked woody cover;

Figure 1(a)), precluding Pearson correlation. Similarly, Pearson correlations were inappropriate from 2014 to 2016, when mean (and median) *S. toltecus* per plot ≤ 1 (several of 24 plots had no *S. toltecus*). In those 3 years of low captures, negative correlation between *S. toltecus* per plot and woody cover were only statistically significant in 2016 ($r_s = -0.477$, $p < .02$, respectively). Bonferroni corrections for Pearson correlations of animals with woody cover where *S. toltecus* occurred in most plots indicated significant negative correlations in 2011 ($r = -0.420$, $p = .041$), 2012 ($r = -0.451$, $p = .027$) and 2013 (-0.516, $p = .01$; e.g., Figure 3). Two-tailed tests assumed that correlations could have been positive (animals favored wooded plots) or negative (animals favored herbaceous cover). Whether individually significant or not, all signs for correlations between woody cover and *S. toltecus* trapped from 2009 to 2016 were negative. A Wald-Wolfowitz Runs Test showed that a series of eight negative signs was unlikely by chance ($p < .001$).

Body Mass and Habitat

Overall, body mass did not reflect year or habitat among adult *S. toltecus*. Exceptions were reproductive (lactating or pregnant) females from 2009, when planted treatments began to differentiate from controls, to 2016 (Figure 4). With data pooled across years, reproductive females (99.8 ± 2.0 g, $n = 72$) were larger than non-reproductive adult females (88.0 ± 1.6, $n = 124$, $F(1, 194) = 21.544$, $p < .0001$). Lactating or pregnant females in control plots were about 9 g heavier (105.1 ± 3.3 g, $n = 32$) than lactating or pregnant females in planted plots (95.7 ± 2.4 g, $n = 40$; $F(1, 70) = 5.874$, $p = .018$).

Other species. Other rodents were captured in insufficient numbers to detect habitat or treatment preferences (Table 1). Timing of captures was interesting; 7 of 41 non-*Sigmodon* rodents were captured before 2012; 34 non-*Sigmodon* rodents were captured 2012 to 2016.

Discussion

Results reported here contribute to understanding of the ecology of *S. toltecus* in early forest restoration. The role this rodent plays in plant succession remains unclear; there is no direct evidence in this study that rodents
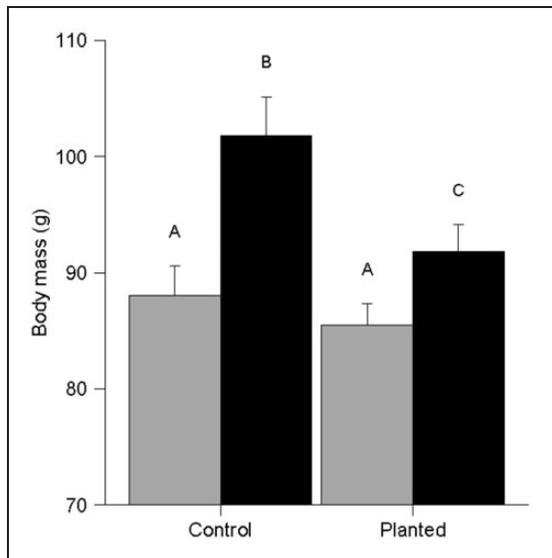
Figure 4. Mean body mass of adult female *S. toltecus* by treatment. Non-breeding female body masses (gray) are indistinguishable in control and planted plots. Reproductive females (black) are significantly larger in controls than in planted plots. Different letters over bars indicate different means with a post-hoc Tukey test at $p < .05$.

alter the course of succession, as microtine rodents do in the temperate zone (Howe et al., 2006; Ostfeld et al., 1997). In contrast to voles, there is no evidence in our study that terrestrial rodents kill planted tree seedlings >15 cm in height. Fossorial gophers (*Orthogeomys hispidus*) sometimes do pull large seedlings and even juvenile plants up to 1 m high into burrows. In a separate exclosure experiment, Guzman and Howe (unpublished) find strong cotton rat suppression of tree recruitment, probably from both seed consumption and herbivory on germinating or small (<10 cm high) seedlings. In the interests of restoration of forest patches from pastures released from agriculture, it is of interest to know which rodents colonize plots.

S. toltecus gained rapid dominance in numbers and biomass from just one individual in 2007 to as many as 149 individuals a subsequent year. Of 697 rodents captured over 10 years, 644 (92%) were this species. Of >46 kg of rodents trapped and released in the years that body masses were recorded, 96% of the biomass was of *S. toltecus*. This result differs from studies of a congener, *S. hispidus*, which is codominant with *Reithrodontomys fulvescens* on the Texas coastal plain (Cameron, 1977). At our site, there was no sign of codominance of *S. toltecus* with other species, either in numbers or biomass. Of the most common other species in the present experiment at Los Tuxtlas, a rice rat (*Oryzomys couesi*), 16 of 17 individuals were captured from 2012 to 2016, but *S. toltecus* was still 5 to 20 times more common than *O. couesi* in those years. Because it outweighed all

but one other species, which was captured only once, *S. toltecus* always represented more biomass and by inference consumption of vegetation than all other species combined.

In Kansas, *S. hispidus* and most other small rodents fluctuate in population numbers on 3 to 5 year cycles (Brady & Slade, 2004). A cycle on that time scale may account for the rapid increase and then decrease in *S. toltecus* between 2008 and 2011; sigmodontine rodents in general and *Sigmodon* in particular host numerous viral and non-viral infectious diseases (Gage, Ostfeld, & Olsen, 1996; Milazzo et al., 2012). Disease might have exacerbated effects of a second severe dry season in 2011. It is clear from coincident and subsequent decline in estimates of the minimum number alive that changes also reflect progression of woody succession accompanied by loss of herbaceous cover.

Densities themselves deserve mention. In a study area of 12 ha of grassy habitat, 20 to 50 *S. toltecus* could have home ranges of 0.60 to 0.24 ha, which would accommodate normal-sized to large-male *S. hispidus* home ranges on the Texas coastal plain (Cameron & Spencer, 1985; Spencer, Cameron, & Swihart, 1990). In the Texas studies, radio transmitters documented home ranges that differed by sex and day as compared with multiday recordings. Even in 12 ha in our study, higher minimum animals alive from 100 to 149 animals, >80% adults, appear cramped. Fur clipping recorded 27 recaptures that could only have occurred by animals leaving the plot where they were first captured, crossing heavily grazed active pasture of grasses <5 cm tall, and entering another plot at least 30 m away (60 m from the center of one plot to the center of another). Fur clipping did not permit rigorous estimates of either movement between plots or home range. Movements by 27 animals probably underestimate mobility. Despite high potential exposure to predation in active pasture (foreground in Figure 1; see Platt, Rainwater, Leavitt, & Miller, 2009), *S. toltecus* may forage on short grazing lawns next to cover. The Texas studies also found exclusivity from home ranges by sex. Aside from a few instances of one adult male and 3 to 4 adult females per plot, which might suggest the equivalent of harems if quantified, exclusivity by sex like that reported in *S. hispidus* was not apparent at Los Tuxtlas.

Decline of *S. toltecus* with decline in herbaceous cover is potentially confounded by population fluctuations for other reasons. Habitat preferences of *S. toltecus* for dense herbaceous ground-cover are evident from trapping patterns and consistent with preferences of *S. hispidus* in Texas (Kincaid & Cameron, 1985). High *S. toltecus* captures occurred before significant forest cover developed in 2010. Even in 2010, high cotton rat numbers that did not show a negative association with shade were probably due to extensive grass cover under and between trees in planted plots (in some planted plots, much like 2009

cover illustrated in Figure 1(a)). In tests of habitat occupation from 2010 to 2012, when repeated measures analysis was feasible, dramatic habitat sorting occurred. Negative associations of this species with woody cover occurred in years after 2010 that had both significant grass and significant woody cover. The 9 g difference in body mass between reproductive females in control and reproductive females in planted plots probably reflects superior food resources in controls, which retained substantial herbaceous cover.

Crowding within plots may be exacerbated by food shortages. Lower densities of smaller voles (*Microtus pennsylvanicus*) devastate edible herbaceous vegetation in the upper Midwest of the United States, in the process creating a largely inedible environment (Howe et al., 2006). In Texas, insects comprise much of the diet for *Oryzomys palustris* and *Reithrodontomys fulvescens*, but *S. hispidus* depends more on plants, especially grasses (Kincaid & Cameron, 1982). In the present study, there is no evidence of extensive herbivory on dominant pasture grasses (exotic *Cynodon dactylon*, *C. plectostachyus*, *Brachiaria brizantha*, *B. decumbens*) or an invasive fern (*Nephrolepis hirsutula*) that form dense ground covers in sun or light shade.

Palatability, and grazer performance, varies widely on these plants. *Cynodon* and *Brachiaria* species are cultivated as pasture grasses around the tropics and in fact are adapted by life history and rhizomatous growth form to survive heavy grazing (Dong & de Kroon, 1997). However, *C. plectostachyus* is cyanogenic and under some circumstances kills cattle and repels wild ungulates (Georgiadis & McNaughton, 1988). C*ynodon dactylon* hosts fungal endophytes that, as in many grasses, produce a wide variety of secondary metabolites that decrease herbivory by insects or mammals (Clay, Holah, & Rudgers, 2005; Latch, 1993; Rudgers et al., 2009). *Brachiaria* species produce many secondary metabolites that repel mammalian herbivores at some times but not at others (Low, 2015). *Nephrolepis hirsutula* is a medicinal fern with a variety of potentially distasteful secondary compounds (Sajeev, Raj, Adarsh, & Hegde, 2015), but palatability to herbivores is not clear. It is plausible to hypothesize that herbaceous cover harboring these rodents is largely inaccessible as food.

Failure to eat dominant herbaceous vegetation does not explain what *S. toltecus* does eat. Exclosure experiments with seed additions of tree species show that recruitment of most native tree species added to experimental plots are strongly suppressed by dense grass cover and by small rodents (almost all *S. toltecus*) 3 km from the site of the present study (Guzman & Howe, unpublished). Given that established tree seedlings >15 to 20 cm in height in the present experiment show no evidence of herbivory by *S. toltecus*, the rodents may subsist on seeds and germinating seedlings from seed

rain of trees and herbaceous vegetation, invertebrates, and perhaps on regenerating new growth of pasture grasses outside the fenced plots. Food scarcity at densities of 6 to 12 *S. toltecus* per $900\,m^2$ habitat patch may be the best explanation of up to 82% trap success in one night. Scarcity is probably exacerbated by season; the annual trapping season in the present study is near the end of a prolonged dry season from March to mid-June.

Woody as contrasted with herbaceous cover also matters. That cover is an important issue with *S. toltecus* is evident from the decline in minimum number alive over 8 years, coincident with huge increases in seed fall and seedling emergence of trees and shrubs between 2007 and 2016 (De la Peña-Domene, Martínez-Garza, Palmas-Pérez, Rivas-Alonso, & Howe, 2014; Martínez-Garza, Flores-Palacios, De La Peña-Domene, & Howe, 2009; Popoca-Ortega, 2016). If seed and seedling influx as food were the sole determinant of performance of this rodent, the minimum number alive would be expected to increase with succession, not diminish to vestigial numbers in small patches of herbaceous cover.

Lessons from trapping during the late dry season over 10 years require context. Like temperate counterparts, populations of these and other tropical rodents are bound to fluctuate seasonally (Brady & Slade, 2004). A short sampling season does not record such changes. Fur clipping that allows identification of recaptures indicates that movements among plots are consistent with those of other small mammals in fragmented habitats (Debinski & Holt, 2000; Diffendorfer, Gaines, & Holt, 1995), but the method only indicates that such movements occur, not how often they occur. Moreover, the minimum number of non-*Sigmodon* rodents present could be underestimated. Trees large enough for small cavities and vine tangles occurred in two plots in 2010, and in several other plots thereafter. Ground trapping may underestimate numbers of rodents that climb easily (*Oryzomys couesi*, *Peromyscus mexicanus*, *Tylomys nudicaudus*; see Reid, 2009). Alternatively, behavioral dominance may explain the low numbers of non-sigmodon rodents. A congener of *S. toltecus*, *S. hispidus*, also traps easily and dominates smaller rodents of the same or different species (Brady & Slade, 2001; Gregory & Cameron, 1988). High capture rates of *S. toltecus* from 2008 to 2013 may have reduced capture of non-*Sigmodon* rodents. Traps quickly commandeered by *S. toltecus* could not be occupied by other species. Larger sizes of recaptured than single-capture individuals and larger reproductive females in control plots with more herbaceous cover than in planted plots are consistent with behavioral dominance in *S. toltecus*.

The ecological role of dominant *S. toltecus* in early restoration remains unclear. In contrast to voles, there is no evidence in our study that terrestrial rodents

kill tree seedlings planted at 15 cm in height. Fossorial gophers (*Orthogeomys hispidus*) sometimes do pull large seedlings and even juvenile plants up to 1 m high into burrows. In a separate exclosure experiment, Guzman and Howe (unpublished) find strong cotton rat suppression of tree recruitment, probably from both seed consumption and herbivory on germinating or small (<10 cm high) seedlings. In the interests of restoration of forest patches from pastures released from agriculture, it is of interest to know whether seed and germinating seedling predation by this species alters the course of succession. That question awaits wider experimentation.

Implications for Conservation

Creation of ecological heterogeneity in agricultural landscapes needs to become a priority for conservation of biodiversity in place, and for facilitating plant and animal migration in the face of climate change (Hernández-Ruedas et al., 2014; Howe, 2016; McConkey et al., 2012; Perfecto & Vandermeer, 2010). Overwhelming dominance of *S. toltecus* in early restoration has implications for relevant land management. Either for reasons of isolation of plots surrounded by inhospitable heavily grazed pasture or behavioral exclusion by super-abundant *S. toltecus*, most other rodents were rare or—like spiny rats (*Heteromys desmarestianus*) in nearby forest—missing in our fenced plots. Evidence that *S. toltecus* has a negative effect on seed and early seedling survival of tree and shrub species that define early tropical succession may prove relevant (Guzman & Howe, unpublished). The degree to which this or other small tropical rodents might slow succession in agricultural landscapes where large areas are abandoned to succession is unclear. Where *S. toltecus* is superabundant, it easily might impede succession in plots released from agriculture. The present study shows that planting trees creates shaded environments conducive to tree and shrub recruitment (De la Peña-Domene et al., 2014). Planting rapidly growing pioneer trees may bypass potentially devastating seed- and early-seedling predation in grassy habitats where *S. toltecus* is common.

Acknowledgments

Author Note

Rodents were handled in accordance with guidelines of the Animal Care and Use Committee (1998) and with University of Illinois Animal Care Protocols (08-161, 08-079, 11-079, 15-082).

Declaration of Conflicting Interests

Funding

References

American Ornithologist Union. (2016). *Checklist of North and Middle American birds*. Retrieved from http://checklist.aou.org

Animal Care and Use Committee (1998). Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy*, 79, 1416–1431.

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P. L., Santos, B. A., Tabarelli, M., & Chazdon, R. (2013). Plant β-diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. *Journal of Ecology*, 101, 1449–1458.

Baker, R. J., & Bradley, R. D. (2006). Speciation in mammals and the genetic species concept. *Journal of Mammalogy*, 87, 643–662.

Bergstrom, B. J., & Rose, R. K. (2004). Comparative life histories of Georgia and Virginia cotton rats. *Journal of Mammalogy*, 85, 1077–1086.

Bradley, R. D., Henson, D. D., & Durish, N. D. (2008). Re-evaluation of the geographic distribution and phylogeography of the *Sigmodon hispidus* complex based on mitochondrial DNA sequences. *Southwestern Naturalist*, 53, 301–310.

Brady, M. J., & Slade, N. A. (2001). Diversity of a grassland rodent community at varying temporal scales: The role of ecologically dominant species. *Journal of Mammalogy*, 82, 974–983.

Brady, M. J., & Slade, N. A. (2004). Long-term dynamics of a grassland rodent community. *Journal of Mammalogy*, 85, 552–561.

Cameron, G. N. (1977). Experimental species removal: Demographic responses by *Sigmodon hispidus* and *Reithrodontomys fulvescens*. *Journal of Mammalogy*, 58, 488–506.

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

Carroll, D. S., & Bradley, R. J. (2005). Systematics of the genus Sigmodon: DNA sequences from beta-fribrinogen and cyctochrome *b*. *Southwestern Naturalist*, 50, 342–349.

Clay, K., Holah, J., & Rudgers, J. A. (2005). Herbivores cause a rapid increase in hereditary symbiosis and alter plant community composition. *Proceedings of the National Academy of Sciences (USA)*, 102, 12465–12470.

De la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S., Rivas-Alonso, E., & Howe, H. F. (2014). Roles of birds and bats in early tropical-forest restoration. *Plos ONE*, 9(8): e104656.

Debinski, D. M., & Holt, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology*, *14*, 342–355.

Diffendorfer, J. E., Gaines, M. S., & Holt, R. D. (1995). The effects of habitat fragmentation on movements of three small mammal species. *Ecology*, *76*, 827–839.

Dong, M., & de Kroon, H. (1997). Plasticity in morphology and biomass allocation in *Cynodon dactylon*, a grass species forming stolons and rhizomes. *Oikos*, *70*, 99–106.

Engilis, A. Jr., Cole, R. E., & Caro, T. (2012). Small mammal survey of Chiquibul Forest Reserve, Maya Mountains, Belize, 2001. *Occasional Papers of the Museum of Texas Tech University*, *308*, 1–23.

Estrada, A., Coates-Estrada, R., & Merrit, D. Jr. (1994). Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography*, *17*, 229–241.

Flores, J. J., Coates, R. I., Sánchez-Cordero, V., & Mendieta, V. J. (2014). Mamíferos terrestres de la Estación de Biologia de Los Tuxtlas. *Revista Digital Universitaria*, *15*, 1–10.

Gage, K. L., Ostfeld, R. S., & Olsen, J. G. (1996). Non-viral vector-borne zoonoses associated with mammals in the United States. *Journal of Mammalogy*, *76*, 695–715.

Garcia-Aguirre, M. C., Alvarez, R., Dirzo, R., Ortíz, M. A., & Eng, M. M. (2010). Delineation of biogeomorphic land units across a tropical natural and humanized terrain in Los Tuxtlas, Veracruz, Mexico. *Geomorphology*, *121*, 245–256.

Georgiadis, N. J., & McNaughton, S. J. (1988). Interactions between grazers and a cyanogenic grass, *Cynodon plectostachyus*. *Oikos*, *51*, 343–350.

Gregory, M. J., & Cameron, G. N. (1988). Examination of socially induced dispersal in *Sigmodon hispidus*. *Journal of Mammalogy*, *69*, 251–260.

Guevara, S., Laborde, J., & G. Sánchez-Ríos, G. (Eds.). (2004). *Los Tuxtlas. El Paisaje de la Sierra*. Xalapa, Veracruz, Mexico: Instituto de Ecología, A.C..

Hernández-Ruedas, M. A., Arroyo-Rodríguez, V., Meave, J. A., Martínez-Ramos, M., Ibarra-Manríquez, G., Martínez, E., . . . Santos, B. A. (2014). Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS ONE*, *9*(6): e98931.

Howe, H. F. (2016). Making dispersal syndromes and networks useful in tropical conservation and restoration. *Global Ecology and Conservation*, *6*, 152–178.

Howe, H. F., & Martinez-Garza, C. (2014). Restoration as experiment. *Botanical Sciences*, *92*, 459–468.

Howe, H. F., Sullivan, A. T., Zorn-Arnold, B., & Brown, J. S. (2006). Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology*, *87*, 3007–3013.

Kincaid, W. B., & Cameron, G. N. (1982). Dietary variation in three sympatric rodents on the Texas coastal prairie. *Journal of Mammalogy*, *63*, 668–672.

Kincaid, W. B., & Cameron, G. N. (1985). Interactions of cotton rats with a patchy environment dietary responses and habitat selection. *Ecology*, *66*, 1769–1783.

Latch, G. C. M. (1993). Physiological interactions of endophytic fungi and their hosts. Biotic stress tolerance imparted to grasses by endophytes. *Agriculture, Ecosystems and Environment*, *44*, 143–156.

Low, S. G. (2015). Signal grass (*Brachiaria decumbens*) toxicity in grazing ruminants. *Agriculture*, *5*, 971–990.

Martínez-Garza, C., Bongers, F., & Poorter, L. (2013). Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management*, *303*, 35–45.

Martínez-Garza, C., Flores-Palacios, A., De La Peña-Domene, M., & Howe, H. F. (2009). Seed rain in a tropical agricultural landscape. *Journal of Tropical Ecology*, *25*, 541–550.

Martínez-Garza, C., Tobon, W., Campo, J., & Howe, H. F. (2013). Drought mortality of tree seedlings in an eroded tropical pasture. *Land Degradation and Development*, *24*, 287–295.

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, *146*(1): 1–13.

Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., & Tabarelli, M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology and Evolution*, *28*, 462–468.

Milazzo, M. L., Cajimat, M., Romo, H. E., Estrada-Franco, J. G., Iñiguez-Dávalos, L., Bradley, R. D., . . . Fulhorst, C. F. (2012). Geographic distribution of Hantaviruses associated with neotomine and sigmodontine rodents, Mexico. *Emerging Infectious Diseases*, *18*, 571–576. DOI: 10.3201/eid1804.111028

Missouri Botanical Garden. (2016). *Tropicos.org*. Saint Louis, MO. Retrieved from http://www.tropicos.org

Ostfeld, R. S., Manson, R. H., & Canham, C. D. (1997). Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology*, *78*, 1531–1542.

Peppers, L. L., Carroll, D. S., & Bradley, R. D. (2002). Molecular systematics of the genus *Sigmodon* (Rodentia: Muridae): Evidence from the mitochondrial cytochrome *b* gene. *Journal of Mammalogy*, *83*, 396–407.

Perfecto, I., & Vandermeer, J. H. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Science of the United States of America*, *107*, 5786–5791.

Platt, S. G., Rainwater, T. R., Leavitt, D. J., & Miller, S. M. (2009). Diet of barn owls (*Tyto alba*) in northern Belize. *Southwestern Naturalist*, *54*, 104–107.

Popoca-Ortega, L. I. (2016). *Lluvia de Semillas en Parcelas de Restauración Ecológica en la Selva Tropical de los Tuxtlas, Veracruz, México*. Tesis de Licenciatura, Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos. Cuernavaca, Morelos, México..

Reid, F. A. (2009). *A field guide to the mammals of Central America and Southern Mexico* (2nd ed.). New York, NY: Oxford University Press.

Rudgers, J. A., Afkhami, M. E., Rua, M. A., Davitt, A. J., Hammer, S., & Huguet, V. M. (2009). A fungus among us: Broad patterns of endophyte distribution in the grasses. *Ecology*, *90*, 1531–1539.

Sajeev, S., Raj, P., Adarsh, D. B., & Hegde, S. (2015). Phytoconstituents of *Nephrolepis hirsutula* and *Ptiygrogramma calomelanos*, two medicinal ferns of the Western Ghats. *Indian Fern Journal*, *32*, 244–256.

San-José, M., Arroyo-Rodríguez, V., & Sánchez-Cordero, V. (2014). Association between small rodents and forest patch and landscape structure in the fragmented Lacandon Rainforest, Mexico. *Tropical Conservation Science*, *7*, 403–422.

Spencer, S. R., Cameron, G. N., & Swihart, R. K. (1990). Operationally defining home range: Temporal dependence exhibited by hispid cotton rats. *Ecology*, *71*, 1817–1822.

Wilson, D. W., & Reeder, D. M. (Eds.). (2005). *Mammal species of the World* (3rd ed.). Baltimore, MD: Johns Hopkins University Press. Retrieved from http://vertebrates.si.edu/msw/mswcfapp/msw/