



# Mating system of *Thrichomys fosteri* in the Brazilian Pantanal: spatial patterns indicate promiscuity

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## Abstract

Animal mating systems provide key insights into the relationship between evolutionary processes and ecological factors such as the spatio-temporal fluctuation of resource abundance. Characteristics of mating systems can be inferred from the spatial distribution of conspecifics and the arrangement of reproductive pairs. Here we used home-range size and overlap for *Thrichomys fosteri* in the Brazilian Pantanal to infer the mating system on this echimyid rodent. Our aims were to verify the existence of sexual dimorphism, to test whether home-range size varied with the sex and body weight of the individuals, to evaluate the degree of home-range overlap, to estimate mean population density, and to infer individuals' mating system. Twenty one individuals (15 males and six females) were radio tracked from 14 to 349 days, with the number of locations by individuals ranging from 19 to 193 locations. There was a male-biased sexual dimorphism in body weight where males were 1.36 times heavier than females. Males' home-range size increased with their body weight, while for females there was no relationship. There was extensive home-range overlap between both sexes, and no evidence of territoriality. Mean population density ranged from 0.9 to 3.03 individuals/ha. Our results indicate that multiple mates were available for both sexes, characterizing a promiscuous mating system.

**Keywords** Density estimation · Home-range overlap · Home-range size · Sexual dimorphism · Rodent

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## Introduction

Mating systems—a cornerstone in the work of Fisher and Darwin (Orians 1969)—have served as a basis to improve our understanding of evolutionary processes because they

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are a major determinant to a population's growth and maintenance (Wynne-Edwards 1962). Despite their importance, however, mating systems are difficult to determine in free ranging species. This challenge is especially daunting for species whose natural history is poorly known, which is the case of most tropical rodents. Thus, mating systems remain a difficult but important challenge in mammal research.

Due to these challenges, mammalogists have historically tried to infer rodent mating systems—promiscuity, monogamy, polyandry or polygyny—based on several observational proxies. Proxies used have varied in quality and resolution, and if the information was gathered from biological entities (i.e., individual or population) or from the environment (i.e., resources). Therefore, inferences have been drawn from proximal evidence such as paternity information (e.g., Asher et al. 2004, 2008) to those more distal, such as body morphology (Heske and Ostfeld 1990; Asher et al. 2008), population parameters (e.g., Adler et al. 1997; Kraus et al. 2003; Asher et al. 2004), behavioral observations (e.g., Guichón et al. 2003; Asher et al. 2004, 2008; Silva et al. 2008), and spatial data (e.g., Adler et al. 1997; Seamon and Adler 1999; Kraus et al. 2003; Asher et al. 2004, 2008; Endries and Adler 2005).

As an example, from a morphometric point of view, researchers have considered sexual dimorphism in body size to be related to the intensity of intrasexual competition for mates (Heske and Ostfeld 1990; Boonstra et al. 1993; Ostfeld and Heske 1993). Male-biased sexual dimorphism should arise within polygyny systems due to intense competition among males for access to females (Schulte-Hestedde 2007). On the other hand, some evidence suggests that the mating system is governed by population density, which in turn is related to home-range distribution and resource availability (Wolff 1985; Adler 2011).

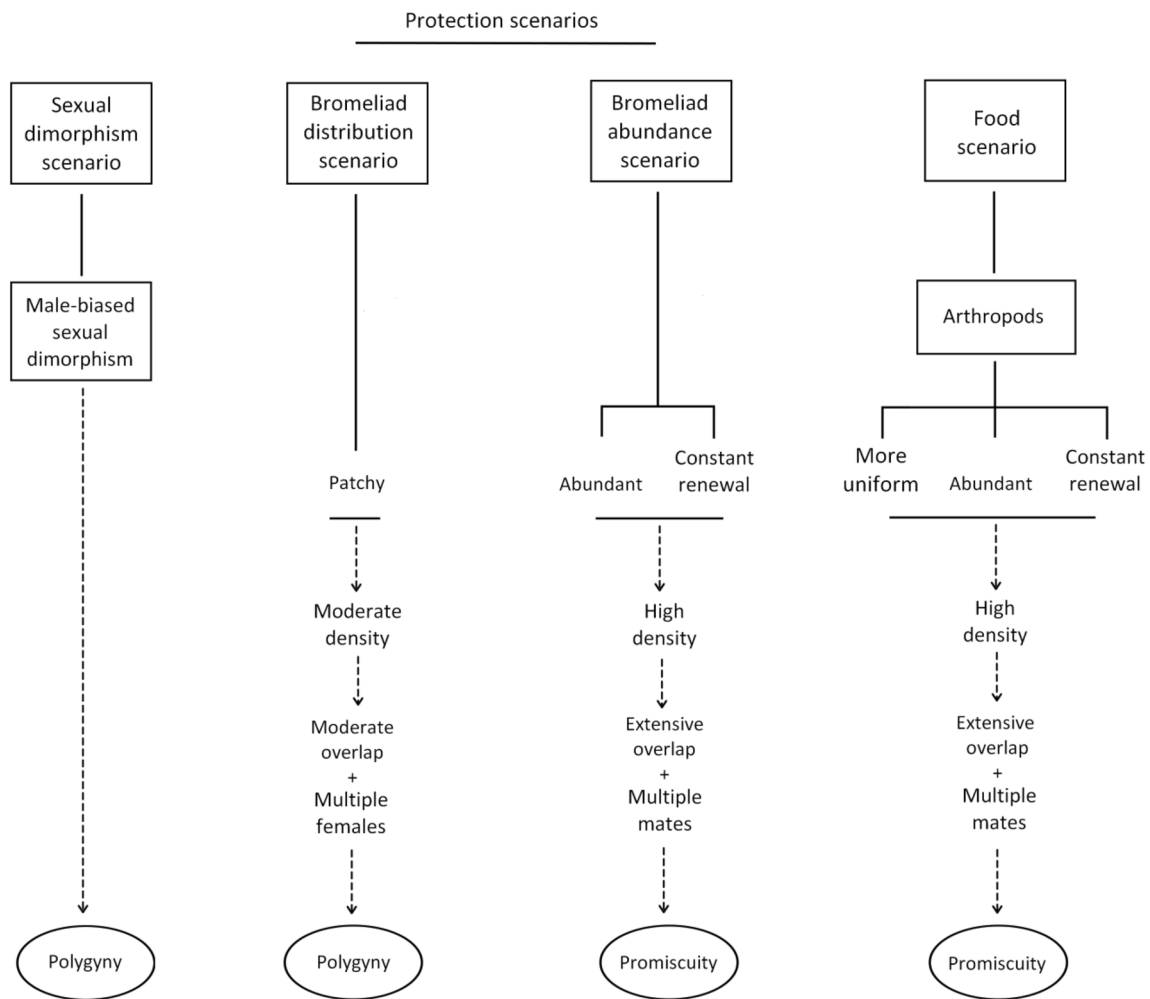
Among rodent species, the family Echimyidae is a particularly interesting group in which to study mating systems because extensive work in the field has identified links among animal densities, home-range distributions, and habitat characteristics. According to Adler (2011), the mating systems of echimyids include monogamy, promiscuity, and polygyny, with the dominant system for a given population primarily depending on population density. He also provided a series of predictions to determine mating systems. Monogamy is expected where resources are scarce, highly concentrated in space, and slowly renewed. In this situation, population densities are usually low, resulting in little overlap of home ranges, and therefore multiple mating is rarely available. On the other hand, a promiscuous system, characterized by multiple mates available for both sexes (Ostfeld 1990; Waterman 2007), is expected with higher population densities when the resources are abundant, uniformly distributed, and quickly renewed. In this case, one would expect extensive overlap in home ranges among individuals

of both sexes, allowing multiple mating opportunities for males and females. In situations with intermediate resources and population densities, a polygynous system is expected. In this system, female reproductive success is limited by the acquisition of enough food resources to reproduce, nurse the offspring (Ostfeld 1985, 1990), and then defend the young from infanticide (Wolff 1993). Males in this system do not invest in parental care; thus, their reproductive success is primarily limited by the number of accessible females (Ostfeld 1985, 1990; Bond and Wolff 1999). As a result, females have small home ranges and are territorial, whereas males have larger home ranges and may or may not be territorial.

Here we use sexual dimorphism in body size, population density, home-range overlap, and habitat features to infer the mating system of a poorly known echimyid species, *Thrichomys fosteri* (Punaré). This species was recently split from *T. pachyurus* (Nascimento et al. 2013), and out of five species of *Thrichomys* in Brazil, *T. fosteri* is the only one found in the Pantanal wetland (D'Elía and Myers 2014) where it is widespread (Alho et al. 1987). This species is scansorial (Lacher and Alho 1989) and occurs mainly in bromeliad stands within forested areas (Antunes et al. 2016). Evidence suggests that it breeds year-round, and reproductive peaks are thought to occur in the dry season (Aragona 2008; Andreazzi et al. 2011). In captivity, sexual maturity is reached around 60 days after birth (approximately 140 g) and litters have an average of 4 cubs of approximately 30 g each, which can live up to 4 years (Teixeira et al. 2005).

Based on the theoretical background provided by Adler's (2011) General Model of Echimyid Mating Systems and existing knowledge of *T. fosteri* biology, we identified four possible scenarios that could describe its mating system (Fig. 1).

1. Sexual dimorphism scenario: evidence of male-biased sexual dimorphism suggests a polygynous system because these systems involve intense competition among males for access to females.
2. Bromeliad distribution scenario: Caraguatá (*Bromelia balansae*) cover determines *T. fosteri* individual habitat selection, because the bromeliad cover provides structural protection against predators (Antunes et al. 2016). This bromeliad has a patchy distribution, which Adler (2011) suggests should lead to a typical polygynous system. Under this system, we expect to find moderate population densities, moderate home-range overlaps, and multiple females available for the same male.
3. Bromeliad abundance scenario: As in scenario 2, the bromeliad stands provide important hiding cover to *T. fosteri*. However, despite its patchy distribution, *B. balansae* is abundant and constantly renewed in this study area. When resources are abundant, Adler (2011) predicts a promiscuous mating system. In this case, we



**Fig. 1** Four scenarios to predict *Thrichomys fosteri* mating system, based on previous knowledge about the species' biology (black lines and squares) and the General Model of Echimyid Mating System proposed by Adler (2011) (dashed lines)

expect high population density, extensive home-range overlap, and multiple mates available to males and females.

4. Food scenario: Arthropods are the main food item of *T. fosteri* (Antunes 2014). This resource is abundant, constantly renewed, and uniformly distributed. Thus, resources with these characteristics should elicit a promiscuous system (Adler 2011); we have the same expectations about density and home-range overlap as we did for the previous scenario.

Our four scenarios result in two possible mating system outcomes, showing that the background theory could not provide unambiguous expectations. Therefore, to distinguish between mating systems, we investigated morphometric and ecological characteristics. Specifically, we aimed to (1) verify the existence of sexual size dimorphism based on body weight; (2) test for effects of sex and weight on home-range

size; (3) evaluate the degree of home-range overlap among individuals of the same sex and between sexes; (4) estimate mean population density year-round, and, (5) infer the mating system based on results of objectives (1), (2), (3) and (4).

## Materials and methods

### Study area

We conducted this study in a forested area at Nhumirim Ranch (18° 57.5' S and 56° 37.1' W, datum WGS84), located in the Pantanal wetland, Brazil. Mean annual rainfall is 1000 mm and mean temperature ranges from 29.1 °C in January from 22 °C in June (EMBRAPA 1984). Unlike most of the Pantanal region, where flooding occurs due to river overbanking, this area is subjected to a flood regime that follows the local annual rainfall, which is characterized by

two sharply distinct seasons. The rainy season (more than 120 mm/month) extends from November to March or April, and the dry season (less than 40 mm/month) extends from June to August (Rodela 2006).

A vegetation mosaic characterizes the landscape, where forests, open woodlands and grasslands are interspersed by temporary and permanent water bodies (Alho et al. 1987). Forests are located on the higher ground not reached by floods. We set up a grid of live traps in an area of forest, where characteristic species of semideciduous seasonal forest occur, such as the acuri palm (*Attalea phalerata*), the Caraguatá bromeliad (*B. balansae*), and a native bamboo (*Guadua paniculata*). Occurrence of these plant species in the forest understory was not uniform, being sparse in some parts of the trap grid and occurring in high-density stands in others. The western boundary of the trap grid coincided with the transition between the forest, i.e., the preferential habitat of *T. fosteri* (Antunes 2009), and the shores of an alkaline pond. The northern, southern and eastern limits of the trap grid partially coincided with habitat transitions from forest to open woodland.

### Animal capture and handling

We captured individuals of *T. fosteri* as part of a long-term capture-mark-recapture (CMR) study developed according to the American Society of Mammalogists guidelines (Sikes et al. 2016) and licensed by the Brazilian Environment Institute, IBAMA (SISBIO number 23116-1). We carried out monthly captures between July 2010 and June 2012 (except March 2011) in a grid of 200 × 240 m (4.8 ha). The grid was composed of 143 capture sites separated by 20 m. Each capture site contained a Tomahawk™ trap (45 × 16 × 15 cm; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) and a Sherman trap (Metalúrgica Miranda, Nova Veneza, Santa Catarina, Brazil), alternating between two sizes (30 × 8 × 9 cm or 43 × 12.5 × 14.5 cm). We placed the traps on the ground, 1–2 m apart from each other. We baited the traps with banana and peanut butter, and the baits were replaced daily. Traps remained open for five consecutive nights. For each captured individual we recorded the date and capture site, sex and body weight. We weighed individuals with a 5 g precision spring scale (Pesola AG LightLine, Baar, Switzerland). Individuals were marked with numerical ear-tags on both ears (National Band and Tag Co., Newport, Kentucky). Twenty-one adult individuals were also tagged with VHF collars (weight < 3% of individual body weight; Telenax®, Playa del Carmen, Mexico).

### Sexual dimorphism

To test for sexual dimorphism within the population, we compared the maximum body weight of all adult male and

female individuals using a *t* test, ran by *t* test() function at stats package of R (R Core Team 2012). We considered individuals to be adults if they had a body weight above the minimum value of reproductively active individuals of each sex (i.e., open vagina for females and scrotal testicles for males). We excluded pregnant and/or lactating females from this analysis.

### Movement tracking

We obtained individuals' locations through two methods: CMR and radio telemetry. For the first method, animals were caught as described in the subsection "Animal capture and handling". We radio-tracked 21 individuals monthly between April 2011 and August 2012 (17 months). Tracking was carried out twice a day, at daytime and at night, with a minimum interval of 2 h between locations. During the capture sessions, we did not track individuals at night to avoid affecting capture success; otherwise we obtained locations throughout 24 h. We tracked the individuals until seeing them or identifying their burrows. When this was not possible, we located animals by removing the antenna from the VHF receiver and reducing the radio gain to less than a half of the maximum gain. We tested this procedure previously, and it guaranteed a location error of less than 3 m. After we found an individual, we determinate its exact location by the distance in meters to the nearest capture site. As all of the capture sites in the grid were numbered and the grid was regular and previously georeferenced, we were able to determine the individual location. We removed all the VHF collars after the end of the study, except for four individuals whose equipment malfunctioned and could not be found.

### Home-range estimation

We estimated the home ranges for all individuals that had at least 15 locations, using both the Minimum Convex Polygon (MCP, Mohr 1947) method and the Kernel Density Estimation (KDE, Worton 1989). For CMR data, we only considered the first capture of each individual in each month to avoid dependence among locations, since the baited traps attract animals and prevent their free movement. For the radio telemetry data, we assumed independence of the locations, because 94% of temporally adjacent pairs were obtained with at least 5 h between them. If the animal did not move between two consecutive locations, the last location was discarded. We performed the KDE using the bivariate normal fixed-kernel method under 95% (home range) and 50% (core home range) probability isopleths. The smoothing parameter (*h*) was set to the mean reference value (href—Worton 1995), estimated separately for each individual ( $\text{href}\bar{X} \pm \text{SD} = 12.43 \pm 8.85$  m). Whenever the home range

included non-contiguous contours generated from only one location, we excluded this location and the resulting area.

In the following analyses, we considered only individuals with sufficient locations to produce stable home-range estimates. We assessed home-range estimate stability by examining a graph of the home-range size estimates (using the MCP) as a function of the number of locations; when the curve reached an asymptote, we considered the home-range area to be “stable”. We performed all home-range size estimates using the `mcp.area()` and `kernel.area()` functions in the `adehabitatHR` (Calenge 2006) package of R (R Core Team 2012).

To test the effects of sex, body weight, and their interaction on home-range size, we performed a generalized linear model with the number of locations as an additional covariate, using the `glm()` function. In this analysis, we estimated home-range size using the 95% kernel isopleth and used the maximum of each individual’s measured weight; both variables were natural log-transformed.

### Home-range overlap

We estimated home-range overlap among individuals of the same sex and of different sexes (dyads: male–female, male–male, and female–female). For this analysis, we only used pairs of individuals that could be neighbors within the monitoring periods (see Supplementary Material 1 for the detailed chronology of radio telemetry for all individuals). The neighborhood criterion was based on the concept of the area of potential exploration by individuals, defined as a circular buffer around the centroid of each individual’s home range, with a diameter equal to the distance between the extreme limits of each animal’s 99% kernel home-range estimate. We considered all individuals whose areas of potential exploitation overlapped to be neighbors (see an example in the Supplementary Material 2). We used the `kerneloverlap()` function (Calenge 2006) with Bhattacharyya’s affinity (BA) method to make all comparisons. The BA method is a symmetric index (i.e., only one value for each pair of individuals) that calculates the similarity between the utilization distributions of different pairs of individuals (see details in Fieberg and Kochanny 2005). Note that BA is not area-based: instead it implicitly accounts for density isopleths by calculating the volume of intersection between pairs of two-dimensional density utilization surfaces. This index ranges from 0 to 1, where values around zero indicate low overlap or overlap of areas rarely used by both individuals, while values around 1 indicate high overlap of areas intensively used by the individuals.

Studies on home-range overlap typically calculate a set of pairwise comparisons among individuals; thus, each individual has several values of overlap. Because  $n$  tracked individuals provide  $(n*[n - 1])/2$  values, this can be considered

pseudoreplication for standard statistical analyses (i.e., there are more values than actual replicates). We avoided this problem by permutation  $t$  tests to determine whether any of the three dyad types had different mean overlap. For a given permutation sample, we randomized the dyad type for all unique pairwise comparisons. A  $t$  statistic (based on unequal sample sizes and unequal variances) was calculated for all three comparisons (MM:FF, MM:MF, FF:MF). This was repeated 10,000 times to generate three null distributions for this statistic. The observed  $t$  statistic for each comparison was then compared to the appropriate null distribution; a difference would be considered significant if it fell outside of the 95% quantile of the null (permuted) distribution.

### Density estimation

Monthly abundance was estimated by analyzing the CMR dataset in a Huggins Robust Design model with full heterogeneity implemented in RMark (Laake 2013). The robust design allowed us to estimate abundance within months (closed population) and survivorship between months (open population), controlling for heterogeneity in capture and recapture probabilities. With this parameterization, capture ( $p$ ), recapture ( $c$ ), survivorship ( $S$ ) and temporary migration (Gamma 1 and Gamma 2) parameters were part of the likelihood formulation, while abundance ( $N$ ) was estimated as a derived parameter. We built models that combined external (accumulated rainfall and moonlight brightness at night of capture) and internal (sex, body weight, and behavior response to first capture [ $p \neq c$ ]) variables as covariates affecting capture probabilities. Behavior response considered individual response to the first capture which could bias abundance estimations. Individuals can get used to handling and bait reward, increasing their chance to be recaptured (“trap-happy individuals”), or get scared and avoid trap locations (“trap-shy individuals”). Therefore, behavior response was incorporated by considering probability of capture ( $p$ ) as different of recapture ( $c$ ) (sensu Otis et al. 1978; but also see Williams et al. 2002), that means once individuals are captured, they can change their propensity to be recaptured. Nightly accumulated rainfall and moonlight brightness were accessed from a meteorological station placed at the study area. Because we were specifically interested in abundance, parameters for survivorship and temporary migration were set to be constant. Note that abundance estimations were not affected by survivorship and migration parameters once abundance was derived from detectability ( $p$  and  $c$ ). Models were ranked based on Akaike Information Criteria (AIC). Models ranked with  $\Delta AIC$  higher than 4 were considered implausible. The parameters for all models with  $\Delta AIC < 4$  were averaged.

We converted abundance into an estimate of density by dividing the monthly estimated abundance ( $N$ ) by the



effective sampled area (ESA). By definition, ESA is wider than the trapping area because outer traps can cover area (i.e., they attract individuals) beyond the polygon limits defined by the outer traps. Therefore we estimated ESA by adding a buffer of radius  $R$  around the sampled area. We calculated  $R$  as the radius of a circle with an area equal to the mean home-range area ( $H$ ) estimated for our radio-tracked population ( $R = \sqrt{H/\pi}$ ; sensu Soisalo and Cavalcanti 2006). Finally, we classified density estimation following Adler (2011): low density estimation  $\leq 5$  individuals/ha, moderate density between 6 and 15 individuals/ha, and high density  $\geq 15$  individuals/ha.

All of the analyses described above were run in program R 2.15.1 (R Core Team 2012), and the significance level for statistical tests was 0.05. For all parametric tests, we checked for homogeneity and homoscedasticity of the residuals to ensure the data met the model assumptions.

## Results

The total effort employed during the 23 months of sampling was 32,890 trap-nights. We captured 126 individuals of *T. fosteri* (73 males and 53 females).

### Sexual dimorphism

We considered females to be adults if their body weight exceeded 175 g and males to be adults if their weight exceeded 165 g. The mean body weight for all adult captured individuals (excluding pregnant and/or lactating females) was  $317 \pm 85$  g ( $\bar{X} \pm \text{SD}$ ) for males ( $n=52$ ) and  $234 \pm 60$  g for females ( $n=24$ ). Males were 1.36 times heavier than females ( $t=4.30$ ,  $df=74$ ,  $p=0.001$ ).

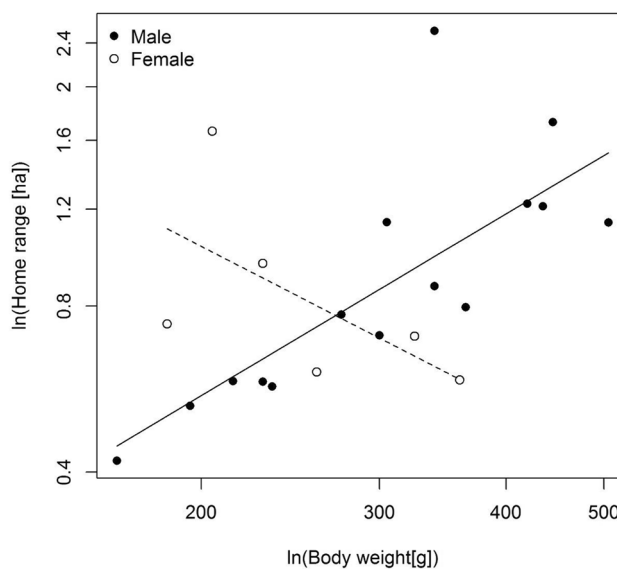
### Home-range size and overlap

We radio-tracked 21 adult individuals of *T. fosteri* (15 males and six females) whose home-range estimates were considered stable, even though individuals were tracked for a short time (see Supplementary Material 3). We assumed that VHF collars had no negative effect on animal health (body weight as a proxy), as all individuals recaptured during the tracking period increased their body weight ( $n=6$ ). We tracked all the individuals for at least 14 days (median = 61 days, ranging from 14 to 349 days,  $n=21$ ), and the number of locations per individual ranged from 19 to 193 (median = 56,  $n=21$ ).

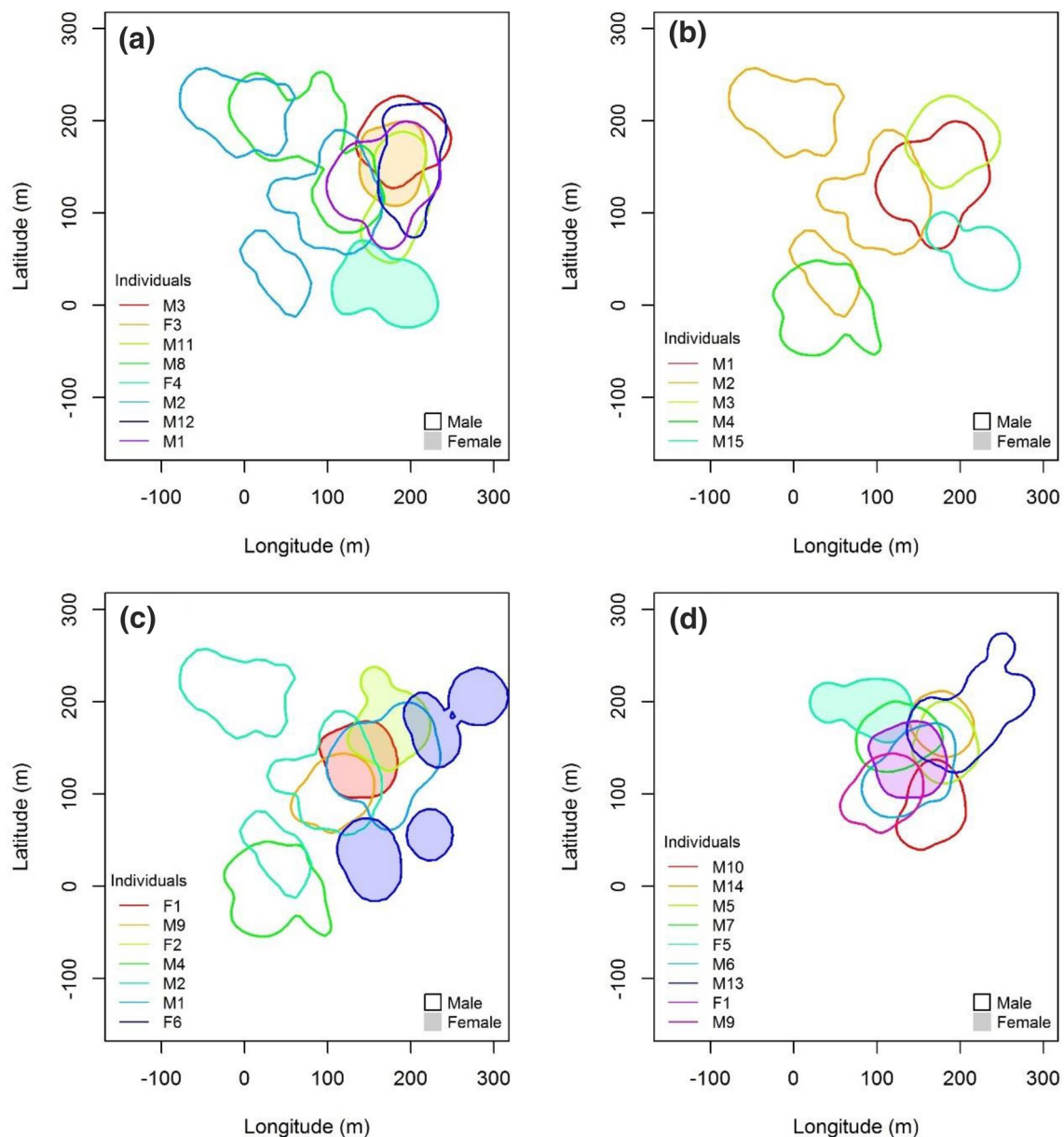
Home-range size was  $0.95 \pm 0.51$  ha ( $\bar{X} \pm \text{SD}$ ,  $n=21$ ), and core home-range was  $0.19 \pm 0.10$  ha ( $n=21$ ). For tracked males, the mean home-range size was  $0.99 \pm 0.55$  ha ( $n=15$ ), and core home range was  $0.20 \pm 0.11$  ha; the mean body weight was 318 g, ranging from 165 to 505 g. For females, mean home-range

size was  $0.88 \pm 0.41$  ha ( $n=6$ ), and core home range was  $0.17 \pm 0.08$  ha; the mean body weight was 260 g, ranging from 185 to 360 g (see Supplementary Material 4). Home-range size was influenced by sex ( $\beta = -1.78$ ,  $t=3.277$ ,  $df=16$ ,  $p=0.005$ ), by body weight ( $\beta = -0.003$ ,  $t=3.910$ ,  $df=16$ ,  $p=0.001$ ), and by the interaction between sex and body weight ( $\beta=0.006$ ,  $t=-3.260$ ,  $df=16$ ,  $p=0.005$ ). The number of locations had no effect on the estimates ( $\beta=0.002$ ,  $t=0.624$ ,  $df=16$ ,  $p=0.541$ ). Males' home-range size was positively affected by body weight ( $\beta=0.003$ ,  $R^2=0.57$ ), while there was no effect for females (Fig. 2).

The bootstrapping test did not reveal any difference in the degree of home-range overlap among dyad combinations ( $p > 0.05$ ): male–female (mean 0.26, range 0–0.84,  $n=18$  pairs), male–male (mean 0.29, range 0–0.79,  $n=46$  pairs) and female–female (zero, 0.15, 0.16, 0.19 and 0.39,  $n=5$  pairs). In all groups of individuals with simultaneous monitoring, there was home-range overlap (based on the 95% kernel isopleth) among individuals of the same sex and opposite sexes. Females' home range was overlapped by more than one male, and the opposite was also true (Fig. 3). For core home ranges, males showed the same overlap pattern, while females did not overlap (see Supplementary Material 5). Most individuals concentrated their home ranges in a specific region of the capture grid, mainly in groups 1 and 4 (Fig. 3a, d, respectively).



**Fig. 2** Relationship between home-range size (estimated by a 95% kernel isopleth) and body weight of 21 adult individuals of *Thrichomys fosteri* tracked between April 2011 and August 2012 in a forest area in the Brazilian Pantanal. Black dots represent males ( $n=15$ ), and white dots represent females ( $n=6$ )



**Fig. 3** Spatial distribution of home ranges (estimated by 95% kernel isopleths) for four groups of adult *Thrichomys fosteri* simultaneously monitored in a forest area in the Brazilian Pantanal. **a** Group 1. **b** Group 2. **c** Group 3. **d** Group 4

### Density estimation

Four models were ranked with  $\Delta\text{AIC} < 4$  and accounted for almost 100% of overall evidence (accumulated  $w \sim 1$ ; Table 1). These models included rainfall and moonlight at night of capture, as well as sex and behavior response to first capture as drivers of heterogeneity in observed catchability ( $p \neq c$ ). Model averaging indicated a strong negative effect of rainfall ( $\beta = -0.28$ , 95% CI  $-0.03$ ,  $-0.54$ ) as well as a trap-shy response to capture ( $c < p$ ;  $\beta = -0.82$ , 95% CI  $-0.51$ ,  $-1.12$ ). On the other hand, sex ( $p_{\text{male}} < p_{\text{female}}$ ;  $\beta = -0.07$ , 95% CI  $-0.6$ ,  $0.30$ ) and lunar

phobia ( $\beta_{\text{male}} = -0.07$ , 95% CI  $-0.6$ ,  $0.30$ ) presented no clear evidence because the confidence intervals for these averaged coefficient estimates overlapped zero. Monthly abundance estimation varied between 7 and 25 individuals throughout the 23 months of monitoring. The average of home-range area (0.95 ha), if considered circular, resulted in a radius of 55.1 m. Therefore, sampled area (4.8 ha) buffered with  $R$  resulted in an ESA of 7.51 ha, and density estimations ranged from 0.9 to 3.03 individuals/ha. These values are within the range considered to be low density (sensu Adler 2011).

**Table 1** Model ranking for abundance estimation of *Thrichomys fosteri* population in a forest area in the Brazilian Pantanal

Model	<i>k</i>	AICc	ΔAIC	<i>w</i>
<i>p</i> (rain + moon) <i>c</i> (.)	8	2222.5	0.00	0.430
<i>p</i> (rain + moon + sex) <i>c</i> (.)	8	2222.5	0.03	0.423
<i>p</i> (moon) <i>c</i> (.)	7	2225.7	3.22	0.086
<i>p</i> (sex) <i>c</i> (.)	7	2226.4	3.90	0.061
<i>p</i> (rain + weight) <i>c</i> (.)	8	2260.6	38.15	0.000
<i>p</i> (rain + sex + weight) <i>c</i> (.)	9	2262.1	39.56	0.000
<i>p</i> (rain + moon + weight) <i>c</i> (.)	9	2262.1	39.57	0.000
Full	10	2263.3	40.79	0.000
<i>p</i> (weight) <i>c</i> (.)	7	2265.4	42.93	0.000
<i>p</i> (rain) <i>c</i> (.)	7	2266.5	43.97	0.000
<i>p</i> (sex + weight) <i>c</i> (.)	8	2266.8	44.30	0.000
<i>p</i> (moon + weight) <i>c</i> (.)	8	2267.2	44.66	0.000
<i>p</i> (moon + sex + weight) <i>c</i> (.)	9	2268.4	45.88	0.000
<i>p</i> (rain + moon + sex) <i>c</i> (.)	9	2269.7	47.21	0.000
Null	6	2271.2	48.70	0.000
<i>p</i> (moon + sex) <i>c</i> (.)	8	2274.8	52.29	0.000

Parameters: *p* = probability of capture; *c* = probability of recapture. Covariates: rain = nightly accumulated rainfall; moon = moonlight brightness; sex = individual's sex; weight = individual's body weight. *k* number of parameters, AICc corrected Akaike Information Criteria, ΔAIC difference between current model's AIC and best model's AIC, *w* model weight

## Discussion

The home-range size of *T. fosteri* varied by sex and (for males) by body weight. Males followed a widely described pattern in mammals, where larger individuals have larger home ranges to meet their survival requirements; home-range size reflects individual energy demand (McNab 1963; Harestad and Bunnell 1979; Lindstedt et al. 1986; Kelt and Van Vuren 2001). In contrast, female *T. fosteri* did not appear to follow this expected pattern. Small rodent females have their reproductive success limited by the acquisition of enough food resources for reproduction and lactation (Ostfeld 1985, 1990) and by their capacity to prevent infanticide by conspecifics (Wolff 1993). As such, adult females' home-range size could be constrained by their capacity to protect young or nest sites, i.e., increasing home-range area could lead to a higher risk of infanticide, which explain why *T. fosteri* adult females' home-range size did not increase proportionally with body weight. Furthermore, reproductive success of small male rodents depends only on the number of females with which they can mate (Ostfeld 1985, 1990; Bond and Wolff 1999), and large home-ranges allow access to more females.

Adler (2011) reviewed thirteen studies that addressed the spatial patterns of nine species of echimyid rodents (Genera *Proechimys*, *Trinomys*, *Kannabateomys* and *Myocastor*).

Ten of these studies evaluated the effect of sex on home-range size, and in nine studies males had larger home ranges than females. Almeida et al. (2013) also found that adult male *Thrichomys apereoides* had larger daily home ranges than females did during the dry season in an area of semi-deciduous forest. However, none of these studies included the influence of individuals' body weight as a covariate. Because our results show that the effect of body weight on home-range size can depend on sex, the difference between sexes detected in previous studies may have been an artifact of males typically being heavier and therefore needing larger home ranges to supply their energy demands.

The male-biased sexual dimorphism we observed for *T. fosteri* supports a polygynous mating system as predicted in the sexual dimorphism and bromeliad distribution scenarios. However, the low estimated population density should lead to multiple mates rarely being available, which characterizes a monogamous system. Neither morphometric nor density information were sufficient to unambiguously determine the mating system for these animals, so we needed to examine the spatial data. In this study, *Thrichomys fosteri* showed extensive home-range overlap (based on the 95% kernel isopleth) within and between sexes, which clearly suggests that males and females could have multiple mates available, and characterizes a classical promiscuous system. Some females (6 in 18 pairs of male–female overlap) had more than 55% of their home ranges overlapping with males; the overlap could reach almost 84%. Additionally, males of *T. fosteri* did not exhibit territorial behavior, as several of them (11 in 55 pairs of male–male overlap) had more than 50% of their home ranges overlapped by other males and, in some cases, had an overlap of almost 80%. Extensive home-range overlap among males also occurred when we considered core areas. During the daytime monitoring, twice we observed different males using the same burrow on consecutive days. In addition, during the night (i.e., the activity period), we recorded two sequential locations (less than 15 min apart) of two males within a radius less than 5 m from each other. These observations are anecdotal, but they provide additional evidence that males exhibit intra-sexual tolerance in their space use.

Combining both anecdotal and systematic evidence, there is a clear support for a promiscuous mating system, which was predicted by the bromeliad abundance and food scenarios. Multiple mates available for both sexes strongly support promiscuity over both monogamous (multiple mates rarely available) and polygynous (multiple mates available only for males) mating systems.

Male-biased sexual dimorphism is expected in polygynous rodents, due to male–male competition for access to females (Schulte-Hestedde 2007). In promiscuous species, postcopulatory competition should be more important (Heske and Ostfeld 1990; Schulte-Hestedde 2007), as it is



related to differential sperm investment, both in quality and quantity (Waterman 2007). In this context body size loses importance. However, it is not recommended to use body weight alone to test for sexual dimorphism (Ostfeld and Heske 1993; Schulte-Hestedde 2007), because differences in skeletal structure, muscle ratio and corporal fat can result in weight differences even with similar sizes. Males, for example, tend to have more muscle mass; therefore, they may be heavier than similar-sized females (Schulte-Hestedde 2007). In *T. fosteri*, however, we observed that males were 1.36 times (83 g on average) larger than females. This remarkable difference indicates that there is indeed a dimorphism; however, it would be interesting to see if there are also differences in body length and other measurements.

The low population density of *T. fosteri* in the study area should restrict the possibilities of multiple mating for both sexes, resulting in a monogamous system. However, the 21 individuals were concentrated in a specific area of the trapping grid. This area had high bromeliad cover, which is positively selected by *T. fosteri* because this cover can provide a safer habitat (Antunes et al. 2016). This led us to re-evaluate the actual density that tracked individuals experienced. The ecological density of this bromeliad patch (i.e., the estimated number of individuals divided by the area of their preferred habitat) should be greater than the density of the total population, resulting in an extensive home-range overlap with multiple mates available for both sexes. This fact may justify the inference of a promiscuous mating system, making Adler's general model of echimyid mating system plausible in the context of ecological density.

It is important to mention that our study has some limitations. One is the small sample size of females. Unfortunately, females are more difficult to capture than males are, and some females were too light to carry VHF collars. These small samples could affect intrasexual home-range overlap and tolerance results. Also, we were not able to track most individuals for long periods of time due to battery life span of the VHF collars. As such, it was difficult to have a large enough sample size to test for seasonal effects on home-size and overlap. These seasonal effects can be important, because climatic seasons (Endries and Adler 2005; Loretto and Vieira 2005), resource availability (Mares et al. 1976; Scharadin and Pillay 2006), and reproductive seasons (Madison and McShea 1987; Sunquist et al. 1987; Loretto and Vieira 2005) affect the home-range size and distribution of some small mammal species. However, we know that the most important component determining space use by this population of *T. fosteri* is Caraguatá bromeliad cover (Antunes et al. 2016), which has a relatively constant availability throughout our tracking period. Further, *T. fosteri* breeding is reported to occur year-round, reducing the possible impact of seasonal effects. Finally, it is important to emphasize that the evidence we provide about the *T. fosteri*

mating system is inferred from social patterns and must be further confirmed by genetic testing because mating systems based on spatial data do not always match genetic information (Adler 2011; Maher and Burger 2011).

Looking at the big picture, spatial data were indispensable to distinguish scenarios and determine the mating system for a little-studied species. This type of ecological information is more reliable for identifying mating systems than sexual dimorphism and population density because spatial data are direct proxies of the availability of mates. Density estimation could also be a good predictor if one is able to consider habitat selection or preferences and takes an ecological density approach.

## Conclusions

The study population of *T. fosteri* showed male-biased sexual dimorphism. Positive body weight effects on home-range-size were found only for males. Home range and core overlapping patterns suggest that males did not present signs of territorial defense, and both females and males had multiple mates available. The individuals seem to have a promiscuous mating system, which is suggested by the observed space-use patterns and the renewal rate and abundance of critical resources (food and protection). We suggest promiscuity is a result of the high ecological density to which individuals are subjected.

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## References

- Adler GH (2011) Spacing patterns and social mating systems of Echimyid rodents. *J Mammal* 92:31–38. <https://doi.org/10.1644/09-MAMM-S-395.1>
- Adler GH, Endries M, Piotter S (1997) Spacing patterns within populations of a tropical forest rodent, *Proechimys semispinosus*, on five Panamanian islands. *J Zool* 241:43–53. <https://doi.org/10.1111/j.1469-7998.1997.tb05498.x>
- Alho CJR, Campos ZMS, Gonçalves HC (1987) Ecologia de capivara (*Hydrochaeris hydrochaeris*, Rodentia) do Pantanal: I Habitats, densidades e tamanho de grupo. *Braz J Biol* 47:87–97
- Almeida AJ, Freitas MMF, Talamoni SA (2013) Use of space by the neotropical caviomorph rodent *Thrichomys apereoides* (Rodentia: Echimyidae). *Zoologia* 30:35–42. <https://doi.org/10.1590/S1984-46702013000100004>
- Andreazzi CSD, Rademaker V, Gentile R, Herrera HM, Jansen AM, D'Andrea PS (2011) Population ecology of small rodents and marsupials in a semi-deciduous tropical forest of the southeast

- Pantanal, Brazil. *Zoologia* 28:762–770. <https://doi.org/10.1590/S1984-46702011000600009>
- Antunes PC (2009) Uso de habitat e partição do espaço entre três espécies de pequenos mamíferos simpátricos no Pantanal Sul-Mato-Grossense, Brasil. M.S. thesis, Federal University of Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil
- Antunes PC (2014) Ecologia de *Thrichomys fosteri* (Rodentia; Echimyidae) no Pantanal: dieta, área de vida e seleção de recursos. Ph.D. dissertation, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil
- Antunes PC, Oliveira-Santos LGR, Tomas WM, Forester JD, Fernandez FAS (2016) Disentangling the effects of habitat, food, and intraspecific competition on resource selection by the spiny rat, *Thrichomys fosteri*. *J Mammal* 97:1738–1744. <https://doi.org/10.1093/jmammal/gyw140>
- Aragona M (2008) História natural, biologia reprodutiva, parâmetros populacionais e comunidades de pequenos mamíferos não voadores em três habitats florestados do Pantanal de Poconé, MT. Ph.D. dissertation, Universidade de Brasília, Brasília, Brazil
- Asher M, Oliveira ES, Sachser N (2004) Social system and spatial organization of wild guinea pigs (*Cavia aperea*) in a natural population. *J Mammal* 85:788–796. <https://doi.org/10.1644/BNS-012>
- Asher M, Lippmann T, Epplen J, Kraus C, Trillmich F, Sachser N (2008) Large males dominate: ecology, social organization, and mating system of wild cavies, the ancestors of the guinea pig. *Behav Ecol Sociobiol* 62:1509–1521. <https://doi.org/10.1007/s00265-008-0580-x>
- Bond ML, Wolff JO (1999) Does access to females or competition among males limit male home-range size in a promiscuous rodent? *J Mammal* 80:1243–1250. <https://doi.org/10.2307/1383174>
- Boonstra R, Gilbert BS, Krebs CJ (1993) Mating systems and sexual dimorphism in mass in microtines. *J Mammal* 74:224–229. <https://doi.org/10.2307/1381924>
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- D'Elía G, Myers P (2014) On Paraguayan *Thrichomys* (Hystricognathi: Echimyidae): the distinctiveness of *Thrichomys fosteri* Thomas, 1903. *Therya* 5:153–166. <https://doi.org/10.12933/therya-14-182>
- EMBRAPA (1984) Boletim agrometeorológico: cinco anos de observações meteorológicas, Corumbá, MS, 1977–1981. EMBRAPA, UEPAE de Corumbá, Corumbá
- Endries MJ, Adler GH (2005) Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), in Panama. *J Zool Lond* 265:147–155. <https://doi.org/10.1017/S0952836904006144>
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTI\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTI]2.0.CO;2)
- Guichón ML, Borgnia M, Righi CF, Cassini GH, Cassini MH (2003) Social behavior and group formation in the coypu (*Myocastor coypus*) in the Argentinean Pampas. *J Mammal* 84:254–262. [https://doi.org/10.1644/1545-1542\(2003\)084%3c0254:SBAGFI%3e2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084%3c0254:SBAGFI%3e2.0.CO;2)
- Harestad AS, Bunnell FL (1979) Home range and body weight: a reevaluation. *Ecology* 60:389–402. <https://doi.org/10.2307/1937667>
- Heske EJ, Ostfeld RS (1990) Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *J Mammal* 71:510–519. <https://doi.org/10.2307/1381789>
- Kelt DA, Van Vuren DH (2001) The ecology and macroecology of mammalian home range area. *Am Nat* 157:637–645. <https://doi.org/10.1086/320621>
- Kraus C, Künkele J, Trillmich F (2003) Spacing behaviour and its implications for the mating system of a precocial small mammal: an almost asocial cavy *Cavia magna*? *Anim Behav* 66:225–238. <https://doi.org/10.1006/anbe.2003.2192>
- Laake J (2013) RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013-01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., Seattle, WA
- Lacher TE, Alho CJR (1989) Microhabitat use among small mammals in the Brazilian Pantanal. *J Mammal* 70:396–401. <https://doi.org/10.2307/1381526>
- Lindstedt SL, Miller BJ, Buskirk SW (1986) Home range, time and body size in mammals. *Ecology* 67:413–418. <https://doi.org/10.2307/1938584>
- Loretto D, Vieira MV (2005) The effects of reproductive and climatic seasons on movements in the black-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826). *J Mammal* 86:287–293. <https://doi.org/10.1644/BEH-117.1>
- Madison DM, McShea WJ (1987) Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *Am Zool* 27:899–908. <https://doi.org/10.1093/icb/27.3.899>
- Maher CR, Burger JR (2011) Intraspecific variation in space use, group size, and mating systems of caviomorph rodents. *J Mammal* 92:54–64. <https://doi.org/10.1644/09-MAMM-S-317.1>
- Mares MA, Watson MD, Lacher TE (1976) Home range perturbations in *Tamias striatus*. *Oecologia* 25:1–12. <https://doi.org/10.1007/BF00345029>
- McNab BK (1963) Bioenergetics and the determination of home range size. *Am Nat* 97:133–140. <https://doi.org/10.1086/282264>
- Mohr CO (1947) Table of equivalent populations of North American small mammals. *Am Midl Nat* 37:223–249. <https://doi.org/10.2307/2421652>
- Nascimento FF, Lazar A, Menezes AN, Durans ADM, Moreira JC, Salazar-Bravo J, Andrea PSD, Bonvicino CR (2013) The role of historical barriers in the diversification processes in open vegetation formations during the Miocene/Pliocene using an ancient rodent lineage as a model. *PLoS One* 8:e61924. <https://doi.org/10.1371/journal.pone.0061924>
- Orians GH (1969) On the evolution of mating systems in birds and mammals. *Am Nat* 103:589–603. <https://doi.org/10.1086/282628>
- Ostfeld RS (1985) Limiting resources and territoriality in microtine rodents. *Am Nat* 126:1–15. <https://doi.org/10.1086/284391>
- Ostfeld RS (1990) The ecology of territoriality in small mammals. *Trend Ecol Evol* 5:411–415. [https://doi.org/10.1016/0169-5347\(90\)90026-A](https://doi.org/10.1016/0169-5347(90)90026-A)
- Ostfeld RS, Heske EJ (1993) Sexual dimorphism and mating systems in voles. *J Mammal* 74:230–233. <https://doi.org/10.2307/1381925>
- Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. *Wildl Monogr* 62: 3–35. <https://www.jstor.org/stable/3830650>.
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.R-project.org/](http://www.R-project.org/). Accessed 10 May 2013
- Rodela LG (2006) Unidades de vegetação e pastagens nativas do Pantanal da Nhecolândia, Mato Grosso do Sul. Ph.D. dissertation, Universidade de São Paulo, São Paulo, São Paulo, Brazil
- Scharadin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav Ecol* 17:452–458. <https://doi.org/10.1093/beheco/arj047>
- Schulte-Hestedde AI (2007) Sexual size dimorphism in rodents. In: Wolff O, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago Press, Chicago, pp 115–128
- Seamon JO, Adler GH (1999) Short-term use of space by a neotropical forest rodent, *Proechimys semispinosus*. *J Mammal* 80:899–904. <https://doi.org/10.2307/1383258>

- Sikes RS, the Animal Care and Use Committee of the American Society of Mammalogists (2016) Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal* 97:663–688. <https://doi.org/10.1644/10-MAMM-F-355.1>
- Silva RB, Vieira EM, Izar P (2008) Social monogamy and biparental care of the neotropical southern bamboo rat (*Kannabateomys amblyonyx*). *J Mammal* 89:1464–1472. <https://doi.org/10.1644/07-MAMM-A-215.1>
- Soisalo MK, Cavalcanti SMC (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. *Biol Conserv*. <https://doi.org/10.1016/j.biocon.2005.11.023>
- Sunquist MP, Austad SN, Sunquist F (1987) Movement patterns and home range in the common opossum (*Didelphis marsupialis*). *J Mammal* 68:173–176. <https://doi.org/10.2307/1381069>
- Teixeira BR, Roque ALR, Barreiros-Gómez SC, Borodin PM, Jansen AM, D’Andrea PS (2005) Maintenance and breeding of *Thrichomys* (Trouessart, 1880) (Rodentia: Echimyidae) in captivity. *Mem Inst Oswaldo Cruz* 100:527–530. <https://doi.org/10.1590/S0074-02762005000600005>
- Waterman J (2007) Male mating strategies in rodents. In: Wolff JO, Sherman PW (eds) *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago Press, Chicago, pp 28–41
- Williams B, Nichols J, Conroy M (2002) *Analysis and management of animal populations*. Academic Press, Cambridge
- Wolff JO (1985) The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. *Can J Zool* 63:2657–2662. <https://doi.org/10.1139/z85-397>
- Wolff JO (1993) Why are female small mammals territorial? *Oikos* 68:364–370. <https://doi.org/10.2307/3544853>
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168. <https://doi.org/10.2307/1938423>
- Worton BJ (1995) Using Monte Carlo Simulation to evaluate kernel-based home range estimators. *J Wildl Manag* 59:794–800. <https://doi.org/10.2307/3801959>
- Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh <https://doi.org/10.1126/science.138.3548.1389-a>

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