



## Ecology and social biology of the southern three-banded armadillo (*Tolypeutes matacus*; Cingulata: Chlamyphoridae)

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Basic knowledge of species biology and ecology is essential for the assessment of species conservation status and planning for efficient conservation strategies; however, this information is not always readily available. Here we use movement behavior to understand the ecology and social biology of the poorly known southern three-banded armadillo (*Tolypeutes matacus*). We used VHF and GPS telemetry to monitor 26 individuals from two sites in the Pantanal wetlands of Brazil. We characterized armadillo activity patterns, evaluated the relationship between sex and body mass with home range size and mean daily distance traveled, and examined home and core range overlap. Three-banded armadillos were active on average for  $5.5 \pm 2.8$  h/day, with most of their activity concentrated in the first half of the night. Adult males were heavier and had larger home ranges than adult females. Home range size scaled positively with body mass for males, but not for females. Core ranges for females overlapped little ( $< 1\%$ ) regardless of age, but home ranges for males overlapped both with other males (12%) and females (18%). Our data suggest that three-banded armadillos are mainly a nocturnal species. Home range and spacing patterns point to a generally asocial behavior and a polygynous or promiscuous mating system. We hope that the data generated as a result of this project will contribute to this species' conservation in Brazil and elsewhere by guiding future management and research efforts.

Key words: activity pattern, Cingulata, conservation, daily distance traveled, GPS telemetry, home range, home range overlap, Pantanal, spatial ecology, Xenarthra

O conhecimento básico a respeito da biologia e ecologia é essencial para a avaliação do status de conservação de espécies e o planejamento de estratégia de conservação eficientes, no entanto, estas informações nem sempre estão prontamente disponíveis. Aqui, usamos o comportamento de movimentação para entender a ecologia e a biologia social do pouco conhecido tatu-bolinha (*Tolypeutes matacus*). Utilizamos telemetria VHF e GPS para monitorar 26 indivíduos em duas localidades do Pantanal Brasileiro. Nós caracterizamos os padrões de atividade do tatu-bola, avaliamos a relação entre sexo e massa corporal com o tamanho da área de vida e a distância média diária percorrida, e examinamos a sobreposição de áreas de vida e áreas núcleo. Tatus-bolinha estiveram ativos em média por  $5.5 \pm 2.8$  horas por dia, com maior parte de sua atividade concentrada na primeira metade da noite. Machos adultos foram mais pesados e apresentaram áreas de vida maiores que fêmeas adultas. O tamanho da área de vida aumentou de forma positiva com a massa corporal para machos, mas não para fêmeas. Fêmeas não compartilharam suas áreas de vida e áreas núcleo com outras fêmeas ( $< 1\%$ ), independente da classe etária, enquanto que as áreas de vida ocupadas por machos sobrepuseram com ambos machos (12%) e fêmeas (18%). Nossos dados sugerem que os tatus-bolinha são primariamente noturnos. Sua área de vida e padrão de sobreposição apontam para um comportamento em

geral não-social e um sistema reprodutivo polígino ou promíscuo. Esperamos que as informações geradas aqui contribuam para a conservação desta espécie no Brasil e em outros lugares, orientando futuros esforços de manejo e pesquisa.

Palavras-chave: área de vida, Cingulata, conservação, distância diária percorrida, ecologia espacial, padrão de atividade, Pantanal, sobreposição de área de vida, telemetria por GPS, Xenarthra.

Factual knowledge on species biology and ecology is key to develop efficient conservation strategies to deal with the most critical contemporary ecological problems (Greene 2005; Beyer et al. 2010). Despite its richness (20 recognized species—Abba et al. 2015; Feijó and Cordeiro-Estrela 2016) and broad distribution throughout the Neotropics, the ecology and biology of most Cingulata (armadillo) species is poorly known (Superina et al. 2014). Information on home range measures, population size, natural history, and types of threats, are scarce or nonexistent for some species (Abba and Superina 2010; Superina et al. 2014; Loughry et al. 2015). Armadillos are fossorial and semifossorial animals and have the habit of excavating the soil to build burrows, where they can spend 80–99% of their time (McDonough and Loughry 2008; Maccarini et al. 2015; Desbiez et al. 2018). They are known to be primarily solitary, with rare social interaction, concentrated in the breeding season and during parental care (McDonough 1997; Desbiez et al. 2006; Superina and Abba 2018). The combination of these characteristics hinders the detection and study of armadillos in the wild and contributes to the paucity of studies on their ecology (Loughry and McDonough 2013a).

The southern three-banded armadillo (*Tolypeutes matacus* Desmarest, 1804; hereafter three-banded armadillo) is found primarily in the dry forests of the central region of South America (Feijó et al. 2015), e.g., western Brazil, Bolivia, Paraguay, and Argentina (Wetzel et al. 2008). For both species of the genus *Tolypeutes* [*T. matacus* and *T. tricinctus* (Linnaeus, 1758)], adults weigh between 1.1 and 1.5 kg, and the uniparous females are solely responsible for the care of the young (Eisenberg and Redford 1999). *Tolypeutes* are believed to be active throughout the day and night (Eisenberg and Redford 1999), and *T. matacus*, although mainly nocturnal, shows an increase of diurnal activity at low temperatures (Attias et al. 2018). Both species can dig burrows and build other types of shallow shelters, such as straw nests, for resting (Attias et al. 2016).

While there is more information published on *T. matacus* than on its congener, most of this information is derived from captive animals (e.g., Bernier 2003); dead animals (e.g., Bolkovic et al. 1995); occasional observations (e.g., Sanborn 1930); and fieldwork not focused on the study of the species (e.g., Cuellar 2008). Furthermore, most studies that address the species' ecology in the wild are derived from a single region in the Bolivian Chaco (Cuellar 2002, 2008; Barrientos and Cuellar 2004; Noss 2013). These studies provide most of the existing information on the species' ecology in the wild (e.g., morphology, population density, area of use, daily displacement, and activity and feeding behavior); however, much remains to be learned.

*Tolypeutes matacus*, along with its congener, the Brazilian three-banded armadillo (*T. tricinctus*), are the only armadillos that can roll into a ball as a defense mechanism (Eisenberg and Redford 1999). However, this behavior facilitates its capture by humans and increases the vulnerability of both species to hunting. Together with habitat loss, this vulnerability has contributed to population declines in recent years (Abba and Superina 2010). The three-banded armadillo is classified as Near Threatened (A2cd) by the IUCN Red List of Threatened Species (Noss et al. 2014) and as Data Deficient in Brazil (Reis et al. 2015) because, until now, only one study on its biology has been carried out in the wild in that country (Attias et al. 2016; Attias et al. 2018). The creation of a National Action Plan for the conservation of three-banded armadillos (PAN Tatu-bola—ICMBio 2017) further highlights the priority of conservation efforts toward this species in Brazil. One of the specific goals of the action plan is to broaden the knowledge on the biology and ecology of the species to guide species-specific conservation strategies at a national level.

Biological characteristics and ecological functions of species can be inferred through the study of their movement patterns (Cagnacci et al. 2010). Activity patterns, home range, and daily displacement metrics can reflect how species interact with different components of the environment (e.g., conspecifics, predators, resource availability, and abundance—Pianka 1973; Harestad and Bunnell 1979; Beyer et al. 2010). These measures also reflect species energetic requirements and constraints, and are related both to individual body mass and the species' ecology (e.g., dietary habits—Garland 1983; Carbone et al. 2005; Tucker et al. 2014). Species of the genus *Tolypeutes* have some of the lowest basal metabolic rates among placental mammals (31% of what would be expected for its body mass) and, like the other species of the subfamily Tolypeutinae, are classified as myrmecophagous (McNab 1985; Redford 1985). McDonough and Loughry (2008) speculated that this diet specialization forces these species to range widely in search for ants and termites, generating large dispersed home ranges and few social interactions, a phenomenon confirmed by Desbiez et al. (2020).

Behavioral strategies of space use and activity can be some of the most effective and generalized ways to minimize the influence of unfavorable biotic and abiotic factors and to maximize the access to food and other resources (Layne and Glover 1985). These strategies can vary within a population according to individual characteristics that may shape its needs, such as sex and age class (Imansyah et al. 2008; Saïd et al. 2012). When studying elusive burrowing mammals, data on space use by conspecifics also can help illuminate their spatial organization and mating system (Clutton-Brock 1989). Because

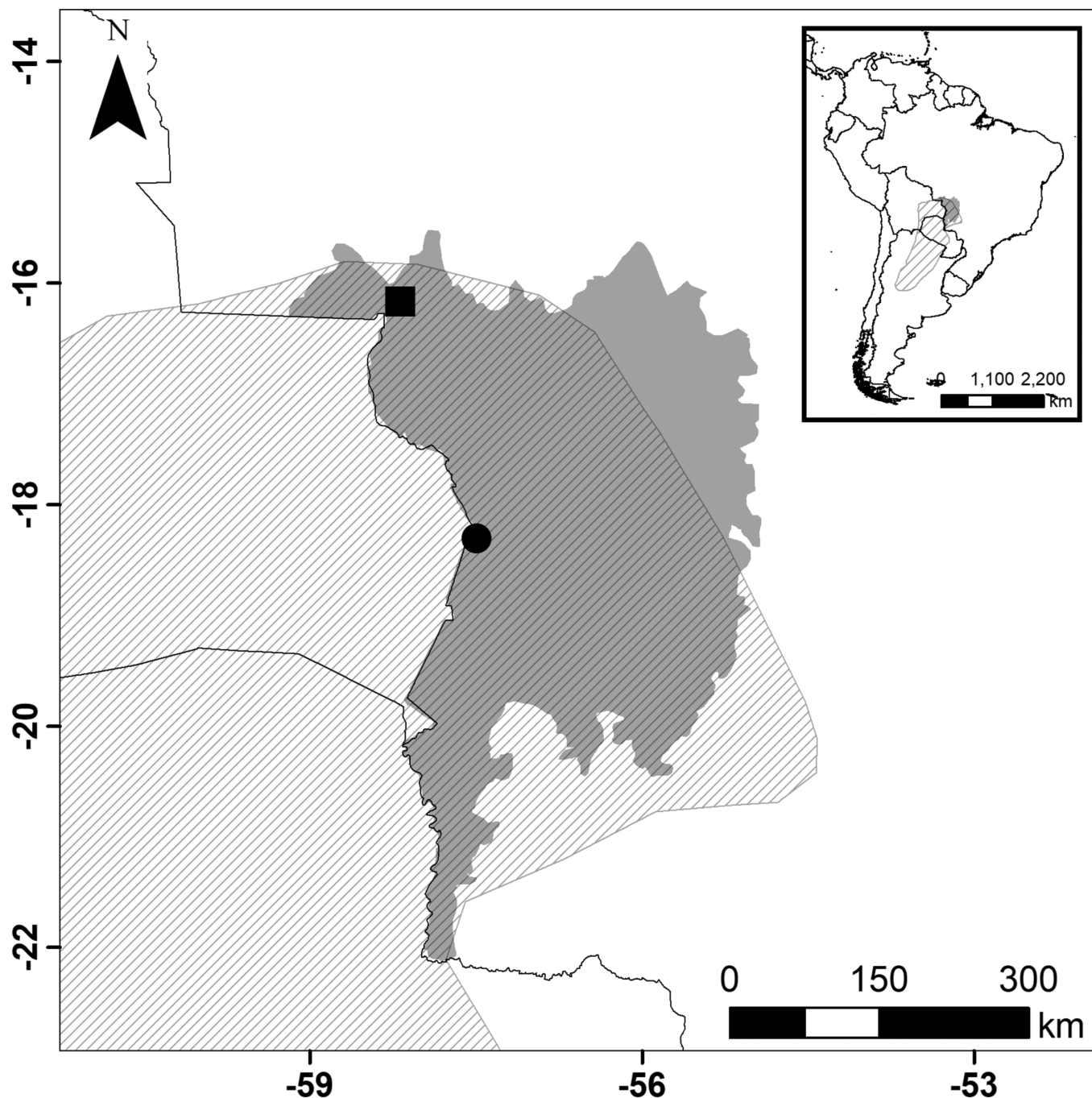
mating systems are, among other factors, related to the defensibility of females by males, they often can be inferred by evaluation of home range sizes and the degree of home range overlap between individuals of the same sex and of opposite sexes (Clutton-Brock 1989; McDonough and Loughry 2008).

Given the uniqueness, current conservation status, and limited published information on three-banded armadillo, our goal was to characterize and understand aspects of the spatial ecology, activity patterns, and social biology, of the species. More specifically, we aimed to estimate measures of space

use and characterize activity patterns, evaluating how these features vary according to individual age class, body mass, and sex.

## MATERIALS AND METHODS

*Study area.*—This study was carried out in the Pantanal wetlands of Western Brazil (Fig. 1). The Pantanal is one of the largest continuous Neotropical wetlands and is located in a low-land floodplain of the upper Paraguay River (Mittermeier et al.



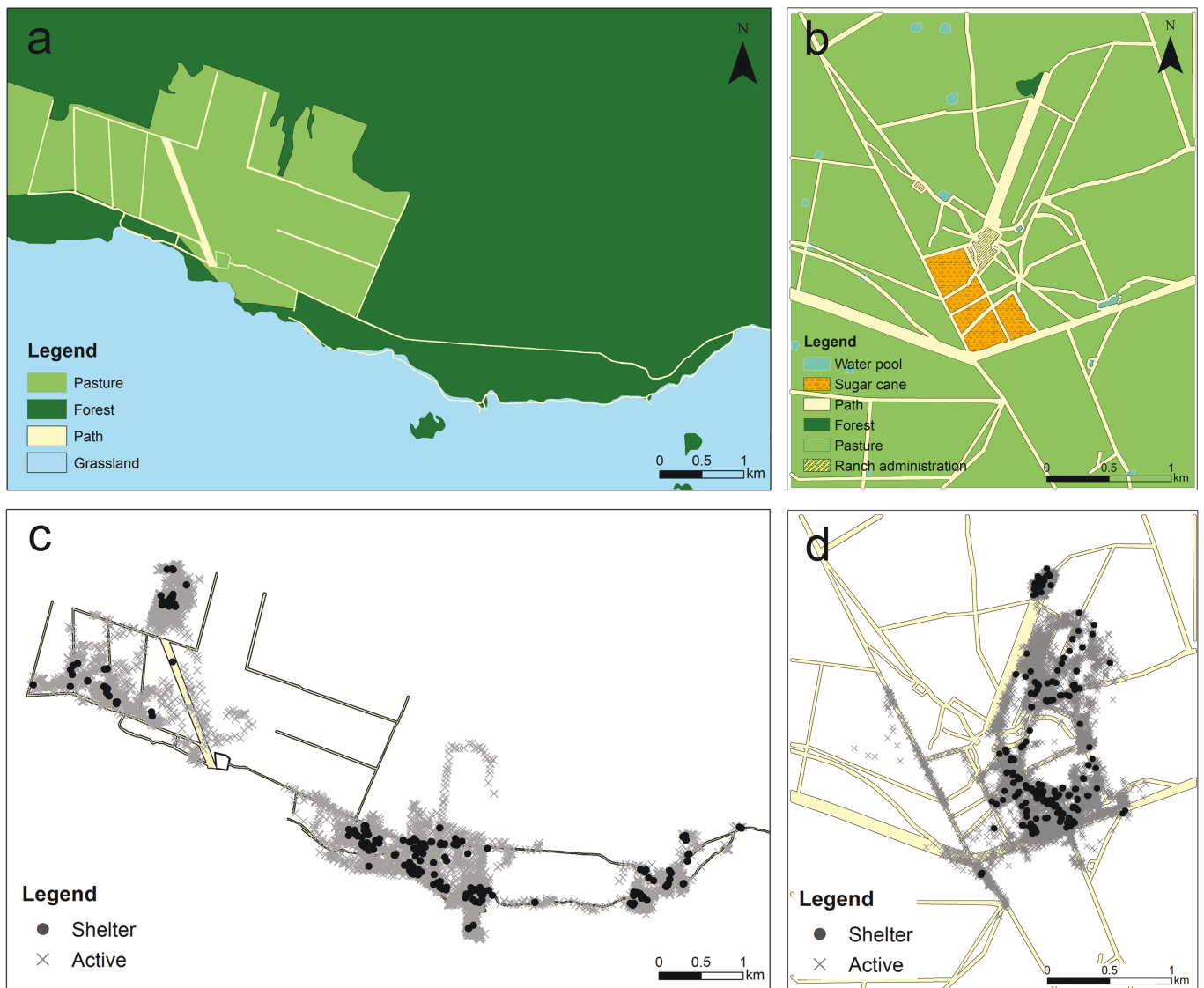
**Fig. 1.**—Location of the study Site 1 (circle, 18°17'51"S, 57°30'35"W) and study Site 2 (square, 16°10'13"S, 58°11'12"W) in the Pantanal (gray area), on the border of Brazil, Bolivia, and Paraguay. The inset figure shows the location of the Brazilian Pantanal (gray area) in South America. In both images, the dashed area indicates the known distribution of *Tolypeutes matacus* according to IUCN.

2003). The region is classified by Köppen's system as tropical subhumid (Aw), with average annual rainfall of 1,100 mm and mean annual temperature of 25°C.

We worked in two sites, 250 km apart (Fig. 1) that are managed in two very different ways: prioritizing the maintenance of the natural landscape (Site 1) versus farming activities (Site 2; Fig. 2). Site 1 (Santa Teresa Ranch) is located in the region of the Amolar Mountain Ridge, in the western limits of the Brazilian Pantanal, Corumbá municipality, Mato Grosso do Sul state (Fig. 1). The variable relief (90–1,000 m of altitude) of this mountainous region defines the vegetation structure. Pastures and humid and dry savannas occupy the lowland areas, which may remain flooded during the flood season (November to April). Natural grasslands remained flooded for most of our study period, except for the short period of late January and early February 2015. The higher areas are dominated by

deciduous and semideciduous forests (Tortato et al. 2015). This 63,000 ha private property is part of the Network for the Protection and Conservation of Serra do Amolar and only 3% of its area has been modified into exotic pasture, dedicated to cattle grazing (Fig. 2). Even though most of this site is preserved forest, armadillos were captured and monitored in both altered and nonaltered habitats, from November 2014 to March 2015.

Site 2 (Duas Lagoas Ranch) is located in Cáceres municipality, Mato Grosso state, in a transition zone between the Pantanal and Cerrado ecoregions. This ranch is owned by a company that produces teak (*Tectona grandis*) wood materials, dedicating 4,155 ha of its 7,378 ha to this activity. A portion of the property still holds native vegetation (1,630 ha), consisting of cerrado woodland ("cerradão"), bush savanna ("cerrado"), grassland, and gallery forest. The remaining area is dedicated to cattle ranching and is occupied by exotic pasture (*Brachiaria*



**Fig. 2.**—Landscape structure and locations of *Tolypeutes matacus* at Site 1 and Site 2 at the Pantanal region, Brazil. Thematic habitat map classified according to vegetation features of Site 1 (a) and Site 2 (b). Relocations of 11 individuals monitored at Site 1 between November 2014 and March 2015 (c) and 15 individuals monitored at Site 2 between July and August 2015 (d). Circles indicate shelter locations and crosses indicate relocations of active individuals.

sp.; 1,209 ha) and sugarcane plantation (24 ha; Fig. 2). At this site, individuals were monitored during July and August 2015 and occupied mostly altered areas of exotic pasture and sugarcane plantation.

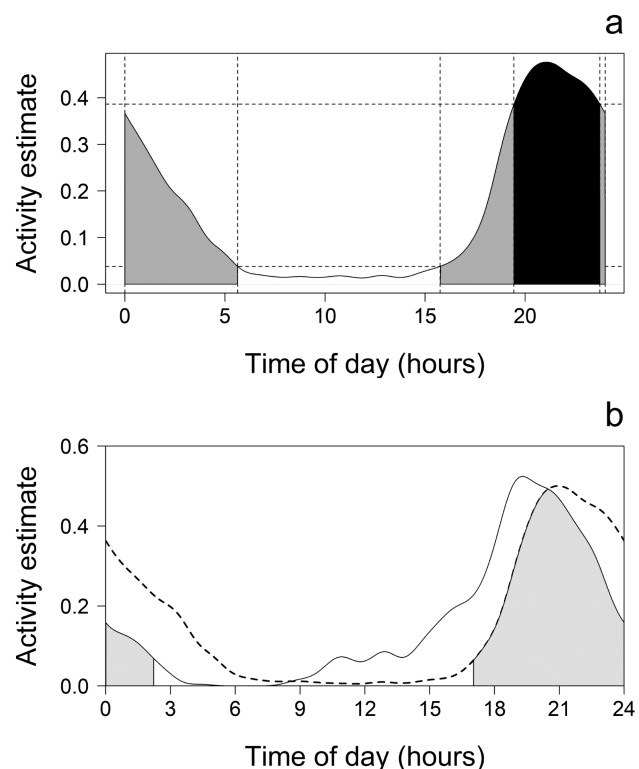
**Capture and tracking methods.**—Following the methods described by Attias et al. (2018), we captured 39 individuals of *T. matacus*, 12 at Site 1 and 27 at Site 2. We undertook active searches and captured animals by hand. From the captured individuals we were able to monitor 11 individuals at Site 1 (7F; 4M) and 15 individuals at Site 2 (7F; 8M). Of the 26 monitored animals, 14 were females (8 adults, 6 juveniles) and 12 males (10 adults and 2 juveniles). Juvenile individuals were defined as those that did not present signs of sexual activity and/or still shared burrows with an adult female. Similar to the pattern described by Desbiez et al. (2019) for *Priodontes maximus*, the field veterinarian identified that juvenile females presented smaller vulvar diameter and poorly developed teats. Based on these external morphological parameters and characteristic behavior, most juvenile individuals were recorded to weigh less than 1 kg. For each individual, we collected information on age, sex, reproductive condition, and body mass. Reproductive condition was assessed only for females, which were inspected for pregnancy through abdominal palpation.

To enable their monitoring, we equipped animals ( $n = 21$ ) with a package containing a glued-on VHF radio (model R1920, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and a GPS tracking device (noncommercial prototype used in other studies of the Wildlife Laboratory of the Brazilian Agricultural Research Corporation of Pantanal—Attias et al. 2018). Total package weight was ~50 g and corresponded to 3–5% of animals' weight. Due to equipment availability or individual circumstances, four juveniles and one pregnant female were equipped only with glued-on VHF radios, which weighed 14 g and corresponded to up to 2% of their weight. Due to the unique behavior and anatomy of this species, we used a protocol that did not prevent the animals from rolling into a ball and attached the tracking devices to the posterior part of the pelvic carapace (Attias et al. 2018). During the short period the devices were allowed to remain attached to the individuals (maximum 32 days), we did not record any significant ulcerations in the carapaces. Individuals were monitored through GPS telemetry, using 5-min interval fixes, and through VHF telemetry, using the homing-in to the animal method (Samuel and Fuller 1994). We tracked animals daily to ensure GPS functioning, animal welfare, record individual behavior and burrow locations. Each animal was tracked at varying times across the days, between 0600 and 2200 h.

Although all the procedures described could be accomplished through physical restraint, to enable the collection of biological samples, some of the animals ( $n = 19$ ) were anaesthetized by an intramuscular injection in the hind limbs (Gasparotto et al. 2017; Attias et al. 2018). All the procedures followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016) and were approved by the ethics committee of the Federal University of Mato Grosso do Sul (process 570/2013).

**Activity.**—To define the activity status of armadillos by the GPS tracks, we used an adaptation of the Residence Time (RT) method (Barraquand and Benhamou 2008) associated with the GPS error pattern, generated whenever an armadillo entered its burrow (hindering GPS reception). An RT time series is obtained by considering the movement portions within circles of a predetermined radius centered at successive locations in an individual's trajectory and computing the duration of the trajectory within that radius for each location. As an extension to the First Passage Time (FPT—Fauchald and Tveraa 2003), the RT calculation allows for brief forays outside of the given circle, as long as they are no longer than a specified time threshold. This method yields particularly clear signals for resting behavior, when an animal spends long periods within a small spatial range (Barraquand and Benhamou 2008). We undertook this analysis using the R package “adehabitatLT” (Calenge 2006), applying a 20-m radius and a 1-h time threshold.

We identified 21,515 activity records from the 61,303 GPS locations of the 21 three-banded armadillos that were GPS-tracked (17 adults and 4 juveniles; Figs. 2 and 3). To characterize timing of activity we used only this GPS data set and



**Fig. 3.**—Kernel density estimates for the activity of *Tolypeutes matacus*. (a) Gray areas represent the activity range (95% Kernel activity density estimates), while the black area represents core activity (50% Kernel activity density estimates) during a 24-h period. (b) Kernel activity density estimates (95%) for juvenile individuals (continuous line) and for adult individuals (dashed line) during a 24-h period. Gray area indicates the activity overlap (67%) between age classes. Data from 21,515 GPS activity records from 21 armadillos tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015.

applied a continuous, nonparametric model of a conditional circular Kernel function (Oliveira-Santos et al. 2013). Kernel density functions provide a continuous measure of the density of data points throughout their distribution (Worton 1987). Much like its use to calculate home ranges, this function allows us to consider the use of time in a continuous probabilistic way, providing a clearer measure of the probability of an animal being active at a given time within its activity period. We used 95% and 50% probabilities to characterize the activity pattern and core activity period, respectively. To characterize the similarity of the activity patterns of individuals between study areas (Site 1; Site 2), sexes (male; female); and age classes (adult; juvenile), we estimated the amount of overlap between the 95% probability distribution of each group (Oliveira-Santos et al. 2013). Finally, we followed the definitions and methods presented by Attias et al. (2018) to estimate activity onset, termination, bout duration, total daily activity duration, and daily rest duration.

**Home range.**—To estimate the home range of the armadillos, we used both GPS and VHF data for all tracked individuals and applied Kernel probabilistic nonparametric models (Worton 1987). Besides emphasizing more stable central tendencies, the final function of the Kernel model identifies peaks of use and less used areas during the monitored period (Powell 2000). Kernel Use Density (KUD) was estimated using a bivariate normal distribution for each Kernel and the same grid for all individuals (grid cells = 400), which ensures that all individual home ranges are plotted over grids with the same resolution and allows comparisons between individual estimates. The fixed smoothing parameter ( $h = 70.97$ ) was estimated as the mean value of the normal reference rule values ( $h_{\text{ref}}$ —Worton 1995) obtained for each individual. In addition, to allow comparison of our results with those of previous studies, we generated home range area estimates through the Minimum Convex Polygon (MCP), a simple estimator that consists of connecting the most external records forming the smallest polygon without concavities (Mohr 1947). MCPs were estimated using both GPS and VHF data gathered for all 26 monitored individuals. To evaluate if MCP 100% estimates differed from those obtained using KUD 95% we used a paired Student's *t*-test. We used MCP estimates to compare the home range size in our study site to those of *T. tricinctus*. We used Welch's *t*-test to assess differences between MCP 100% home range estimates for the two *Tolypeutes* species, based on our results and those of Guimarães (1997). All analyses were carried out using the R package "adehabitatHR" (Calenge 2006).

Scaling of home range with body mass is known for several species (Jetz et al. 2004). To ensure that home range size measures from both study sites could be pooled together for analyses and were not biased by body mass variation between study sites, we used a Student's *t*-test to assess if the body mass and home range size estimates of adult armadillos differed between study areas. Comparisons between study areas were made considering only adults to avoid incorporating the potential confounding effects of body mass on home range estimates. We used the same approach to evaluate differences in

home range size estimates and body mass between sexes. We fitted an ANCOVA model to evaluate the relationship between home range size (KUD 95%), sex, and body mass. Because body mass and sex interacted to explain home range size, we carried out linear regressions for each sex to assess how home range area estimates vary according to body mass.

**Daily distance traveled.**—Daily distance traveled by individuals was estimated using only GPS data and characterized by the cumulative sum of all 5-min step lengths during each day of monitoring. The mean distance traveled was estimated for each individual ( $N = 21$ ) considering its entire monitoring period. We used a Student's *t*-test to assess if the daily distance traveled by adults differed between study areas ( $N = 17$ ). We fitted a linear mixed effects model to assess if daily displacement varied between sexes, accounting for the random nested effects of individual identity, through the R package "nlme" (Pinheiro et al. 2016). To describe the relationship between mean daily displacement and home range area (KUD 95%), we fitted an asymptotic regression model, a three-parameter model with a mean function  $f(x) = c + (d - c)(1 - \exp(-x/e))$  using the "drm" function of the "drc" R package (R Development Core Team 2018). In this model, "*c*" represented the lower limit and was fixed to 0, "*d*" represented the upper limit of the asymptote, and "*e*" represented the steepness of the relationship, indicating how much mean daily displacement increased with every unit increase in home range.

**Home range overlap.**—To characterize what is traditionally described as "home range overlap," here we estimated space use sharing probabilities. These probabilities take into consideration the intensity with which each animal of a pair uses a determined area and are a better proxy for the level of interaction between two individuals than the traditional overlap measures between two home range contours (Fieberg and Kochanny 2005). We estimated the space use sharing probability between individuals during activity and inactivity separately. First, we estimated core (KUD 50%) and home range areas (KUD 95%) of each individual during these two states, active and inactive, using both VHF and GPS data. Then, we estimated the probability of space use sharing between individuals ( $N = 26$ ) at each activity state and home range level separately using the R package "adehabitatHR" (Calenge 2006). To evaluate the probability of space use sharing between pairs of individuals of different sexes and age classes in the four above-described scenarios, we used the Utilization Distribution Overlap Index (UDOI). The UDOI is a symmetric index that measures the amount of overlap relative to two individuals using the same space uniformly, i.e., the joint distribution probability of two individuals. This index equals zero for two home ranges that do not overlap and equals 1 if both UDIs (i.e., use densities) are uniformly distributed and have 100% overlap. However, UDOI can be  $> 1$  if the two UDIs are nonuniformly distributed and have a high degree of overlap, i.e., if two individuals use the space in a similar manner and share areas of high use density. UDOI is a function of the product of two UDIs and assumes that the evaluated animals use the space independently (Fieberg and Kochanny 2005). Finally, we used a Welch's *t*-test to assess if the overlap measures differed between study areas.

RESULTS

Animals were monitored with GPS devices for an average of 17 days ( $SE = 1.76$ ,  $\min = 4$ ,  $\max = 32$ ). This generated an average of 2,919 locations per individual ( $\min = 218$ ;  $\max = 8,248$ ) and a total of 61,303 locations. VHF tracking generated an average of 39 locations per individual ( $\min = 16$ ,  $\max = 62$ ) and a total of 157 locations (Supplementary Data SD1).

**Activity.**—Three-banded armadillos in general were nocturnal, with most activity concentrated in the first half of the night (Fig. 3). Activity patterns were similar between study areas, with 86% overlap, and were pooled together to characterize the species' behavior. During the monitoring period, the activity onset usually occurred between the late afternoon and the beginning of the night (1700 to 2030 h), and activity termination occurred in the second half of the night. Activity bouts lasted from 1 min to 14 h ( $\text{mean} = 3.3 \pm 2.9$  h) and summed to an average daily activity duration of  $5.5 \pm 2.8$  h. Armadillos stayed inside their shelters for long periods, with an average of  $14 \pm 6.7$  h/day and a maximum of 19.7 h/day. Activity patterns of males and females were similar, with 88% overlap. Adults and juveniles presented slightly different activity patterns (overlap = 67%) and juveniles tended to leave shelters earlier (~1800 h) and return earlier (~2215 h) than adults (Fig. 3b).

**Home range.**—Neither the body mass ( $t_{16} = -1.52$ ,  $P = 0.15$ ), nor the home range size of adult individuals differed between the two study sites ( $t_{15} = -1.37$ ,  $P = 0.19$ ). Therefore, we pooled the data from both sites to carry out the analysis. Adult body mass varied between 0.96 and 1.62 kg ( $\text{median} = 1.27$  kg; Table 1). Median adult home range area was estimated at 58.4 ha (14.5–194.9 ha), when using KUD 95%, and at 64.4 ha (3.27–289.14 ha) when using MCP 100%. MCP estimates for *T. matacus* obtained here did not differ from those obtained by Guimarães (1997) for *T. tricinatus* ( $122 \pm 121$  ha) in Northeast Brazil ( $t_{7,9} = 1.01$ ,  $P = 0.34$ ).

Body mass and sex of the armadillos interacted to explain their home range size (Fig. 4;  $F_{(3,17)} = 7.32$ ,  $P = 0.05$ ); we therefore examined the effect of body mass on home range sizes separately for each sex. Home range size of male *T. matacus* was positively related with their body mass (KUD 95% =  $-86.6 + 139.2 \times \text{Body mass}$ ,  $r^2 = 0.35$ ,  $F_{(1,9)} = 4.95$ ,  $P = 0.05$ ), while female home range sizes did not scale with their body mass ( $F_{(1,8)} = 0.008$ ,  $P = 0.93$ ; Fig. 4). Adult males were heavier than adult females (Table 1; Supplementary Data SD1)

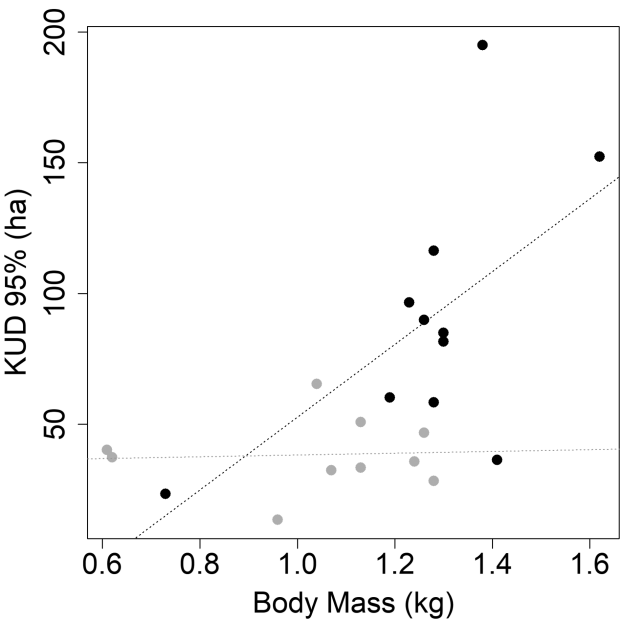
**Table 1.**—Mean and standard deviation of body mass ( $N = 18$ ), Kernel Use Density (KUD) home range size (based on GPS data;  $N = 17$ ), and Minimum Convex Polygon (MCP) home range size (based on GPS and VHF data;  $N = 18$ ) for adult males and females of *Tolypeutes matacus*. Comparison between groups performed through Student's  $t$ -test. Data from adult individuals tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015.

|                | Female        | Male           | $t$   | $d.f.$ | $P$    |
|----------------|---------------|----------------|-------|--------|--------|
| Body mass (kg) | 1.17 (0.12)   | 1.32 (0.12)    | -2.65 | 16     | 0.02   |
| KUD 95% (ha)   | 34.4 (12.25)  | 97.12 (47.11)  | -3.41 | 15     | < 0.01 |
| MCP 100% (ha)  | 28.36 (17.77) | 128.52 (93.20) | -3.20 | 16     | < 0.01 |

and the home range area (KUD 95%) of adult male *T. matacus* was, on average, about 2.8 times larger than the home range area of adult females (Table 1). To allow comparisons with previous studies, we also included the MCP 100% estimates in Table 1, because mean KUD 95% home range estimates differ from mean MCP 100% estimates ( $t_{20} = 2.14$ ,  $P = 0.04$ ).

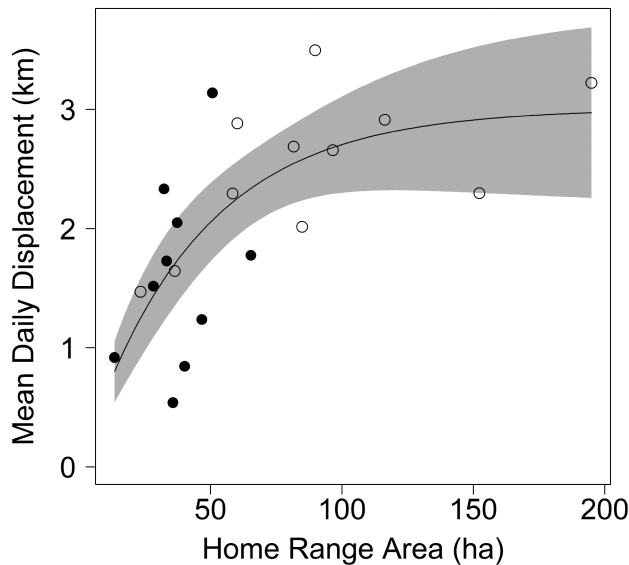
**Daily distance traveled.**—Daily distance traveled by adults did not differ between study sites ( $t_{15} = 1.00$ ,  $P = 0.33$ ). The daily displacement of adults ranged between 0.54 and 3.5 km ( $\text{median} = 2.3$  km). On a daily basis, adult males moved more than adult females ( $t_{19} = 2.77$ ,  $P = 0.01$ ;  $M = 2.67$  km,  $F = 1.52$  km; Table 1). The mean daily displacement was positively related to home range area (Fig. 5). The estimated asymptotic model indicates an asymptote, i.e., an approximate maximum daily displacement, at 3,007 m ( $SE = 385.46$ ,  $P < 0.01$ ) with a steepness ("e"; indicating the increase in meters traveled daily with the increase of 1 ha in the home range area) of 43.5 ( $SE = 12.9$ ,  $P < 0.01$ ).

**Home range overlap.**—Overlap between pairs of individuals did not differ between study sites ( $t_{52,13} = -1.52$ ,  $P = 0.13$ ). Overall, the probability of space use sharing between pairs of individuals was low and was related to sex and age class (Table 2). The average probability of space use sharing was higher when adult animals were active and at home range level (13%), when compared to both inactive periods at home range level (5%) and active periods at core area level (1%; Table 2). During inactive periods, the average probability of space use sharing between animals of different age classes was higher (9%) than that of animals of the same age class (5% for adults and 0 for juveniles) at both home range and core area levels.



**Fig. 4.**—Relationship between body mass (kg) and Kernel Use Density home range size (KUD 95%) of 21 *Tolypeutes matacus* tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015. Black circles represent male armadillos and gray circles represent females. Dotted lines indicated the slope of the linear regressions for each sex.

Females did not share space use at home range or core area level with other females, regardless of age class. The highest average probability of space use sharing between females is 1%, during active periods, at home range level (Table 2). Nevertheless, two juvenile females that were identified as still being nursed by their mothers (through direct observation



**Fig. 5.**—Relationship between mean daily distance traveled and the home range area of 21 *Tolypeutes matacus* tracked at two sites in the Pantanal of Brazil, from November 2014 until August 2015. Home range was estimated by the Kernel method (95%). Black points represent females and white points represent males. The line represents the estimated nonlinear least squares asymptotic model and the shaded area represents the 95% confidence interval.

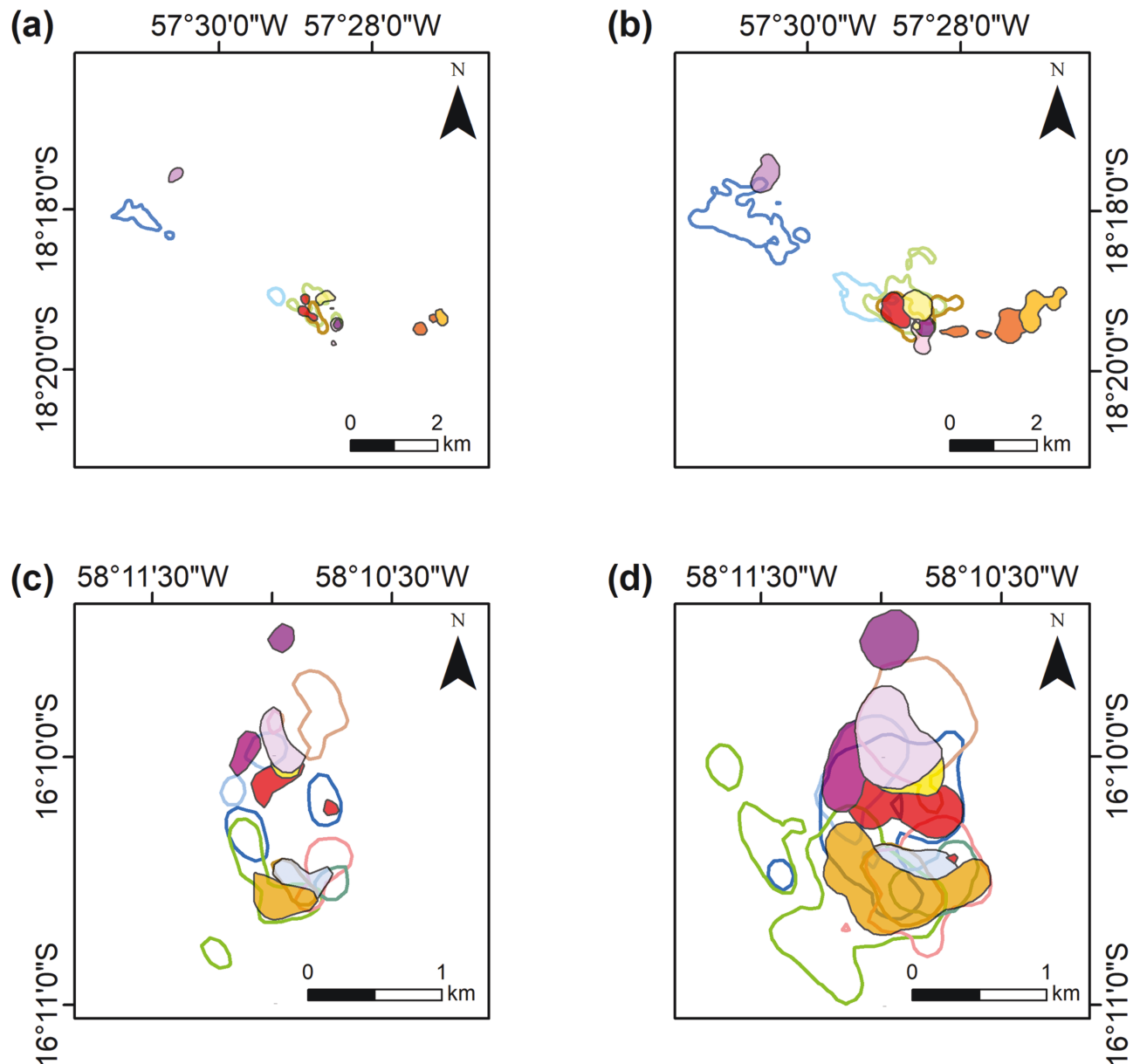
of nursing and burrow sharing), had their home ranges almost completely encompassed by their mother's home range (Fig. 6). Nevertheless, these two juvenile females (TM11 and TM32) only could be monitored through VHF telemetry (Supplementary Data SD1), and space use density probabilities could not be estimated for them and their mothers. When compared to all others, pairs of females showed a lower overlap probability at both home range and core area levels (Table 2). On the other hand, males presented space use sharing with both males and females. In general, the probability of adult intersexual (M-F) space use sharing was higher than the intrasexual probability (Table 2).

## DISCUSSION

**Activity.**—*Tolypeutes matacus* has been reported as a cathemeral species (Eisenberg and Redford 1999), and hunters in the Bolivian Chaco even reported a diurnal activity pattern for the species (Barrientos and Cuellar 2004). Nevertheless, the predicted probability of finding active *T. matacus* during daytime was very low in our study area and they mainly were nocturnal. This pattern is similar to that encountered in the Paraguayan and Bolivian Chaco (Barrientos and Cuellar 2004; Smith 2007; Cuéllar 2008). Furthermore, this nocturnal pattern was observed at both our study sites, showing that this pattern is unlikely to be related to anthropogenic disturbance. In addition, this pattern is similar to that reported for the congener *T. tricinctus*, which also seems to be active at the end of the afternoon and in the first half of the night (Bocchiglieri et al. 2010). Temperature is known to be one of the main factors affecting activity pattern variation in xenarthrans (Mourão and Medri 2007; Maccarini et al. 2015; Attias et al. 2018). The

**Table 2.**—Joint distribution probability of pairs of *Tolypeutes matacus* of different sex and age classes, according to the Utilization Distribution Overlap Index (UDOI). We divided our data set according to the activity status of the individuals ("Active" or "Inactive") and estimated the probability of space use sharing at (a) home range level (KUD 95%) and at (b) core area level (KUD 50%) for each subset of locations. Data from 26 individuals tracked at two sites in the Pantanal of Brazil from November 2014 until August 2015.

| (a)           |              |              |                |              |                   |          |                 |       |
|---------------|--------------|--------------|----------------|--------------|-------------------|----------|-----------------|-------|
| Sex           | Adult–adult  |              | Adult–juvenile |              | Juvenile–juvenile |          | Activity status | Mean  |
|               | Active       | Inactive     | Active         | Inactive     | Active            | Inactive |                 |       |
| Female–female | 0.022        | 0.007        | 0.003          | 0            | 0                 | 0        | Active          | 0.017 |
|               |              |              |                |              |                   |          | Inactive        | 0.005 |
| Female–male   | 0.096        | 0.038        | 0.079          | 0.074        | 0                 | 0        | Active          | 0.177 |
|               |              |              |                |              |                   |          | Inactive        | 0.099 |
| Male–male     | 0.051        | 0.023        | 0.087          | 0.045        | 0                 | 0        | Active          | 0.121 |
|               |              |              |                |              |                   |          | Inactive        | 0.061 |
| <b>Mean</b>   | <b>0.127</b> | <b>0.054</b> | <b>0.12</b>    | <b>0.094</b> | <b>0</b>          | <b>0</b> |                 |       |
| (b)           |              |              |                |              |                   |          |                 |       |
| Sex           | Adult–adult  |              | Adult–juvenile |              | Juvenile–juvenile |          | Activity status | Mean  |
|               | Active       | Inactive     | Active         | Inactive     | Active            | Inactive |                 |       |
| Female–female | 0.001        | 0.007        | 0              | 0            | 0                 | 0        | Active          | 0.001 |
|               |              |              |                |              |                   |          | Inactive        | 0.005 |
| Female–male   | 0.007        | 0.038        | 0.007          | 0.074        | 0                 | 0        | Active          | 0.014 |
|               |              |              |                |              |                   |          | Inactive        | 0.099 |
| Male–male     | 0.003        | 0.023        | 0.002          | 0.045        | 0                 | 0        | Active          | 0.007 |
|               |              |              |                |              |                   |          | Inactive        | 0.061 |
| <b>Mean</b>   | <b>0.009</b> | <b>0.054</b> | <b>0.009</b>   | <b>0.094</b> | <b>0</b>          | <b>0</b> |                 |       |



**Fig. 6.**—Spatial organization and overlap between males (empty polygons) and females (filled polygons) of *Tolypeutes matacus*. Individuals were tracked in two sites in the Brazilian Pantanal, from November 2014 until August 2015. (a) Core area (Kernel 50%) and (b) home range contour (Kernel 95%) of 11 individuals tracked at Site 1. (c) Core area (Kernel 50%) and (d) home range contour (Kernel 95%) of 15 individuals tracked at Site 2.

activity of *T. matacus* can be influenced by air temperature, with an earlier onset and shorter duration at colder temperatures (Attias et al. 2018). We did monitor animals along a broad temperature spectrum at our study site and show that the species' overall activity pattern is indeed nocturnal. In addition, even though we only monitored animals during 7 months of the year, we should not expect great variation from the observed activity pattern due to photoperiod variation, because this is minor in the tropics when compared to temperate zones. Hence, although the diurnal pattern reported by hunters likely was biased by a diurnal hunting effort (Barrientos and Cuellar 2004; Cuéllar 2008), future studies on the activity patterns of *Tolypeutes* sp. should highlight the temperatures experienced

by the animals during the monitoring period to help disentangle the geographical and environmental components of activity pattern variation.

Although we were able to monitor only a few juvenile individuals, it was possible to observe that they tended to leave shelters earlier than did adults. Juveniles of this species have been reported to have diurnal activity patterns on warm winter days in Paraguay (Meritt 2008). In the United States, young nine-banded armadillos (*Dasypus novemcinctus*) also tend to be more diurnal than adults (Layne and Glover 1985; McDonough and Loughry 1997). Differences in activity timing between age classes can be related to predation risk (McDonough and Loughry 1997). Most carnivores in this region are nocturnal

(Astete et al. 2008), and an earlier activity onset by juveniles potentially could reduce their chance of encounters with most putative predators. Adult three-banded armadillos are likely to be preyed upon only by large carnivores that have the strength to puncture their thick carapace or a mouth large enough to engulf the entire rolled animal (e.g., jaguars and maned wolves—Hannibal et al. 2015; A. Bocchiglieri, Universidade Federal de Sergipe, pers. comm.). Younger individuals are more vulnerable to predation by these and other smaller carnivores, due to their relatively softer carapace and smaller size. Differences in activity timing also could be related to variations in body mass between age classes and its consequences for thermoregulation (McNab 1980), i.e., individuals of smaller size and body mass have less thermal inertia with a higher rate of heat loss, especially in the cooler nights. Finally, behavioral and, consequently, niche changes during the life cycle of a species influence intraspecific competition and population dynamics (Ebenman 1987). Differences in activity timing between age classes therefore could reduce intraspecific competition during foraging activities and/or aggressive behavior toward juveniles.

*Home ranges, interactions, and reproductive behavior.*—Home range size is related to the energetic requirements of a species, intra- and interspecific interactions, habitat productivity, and resource patchiness (Harestad and Bunnell 1979). Comparison of home range estimates of adult *T. matacus* obtained in this study (MCP 100% =  $90.4 \pm 82.9$  ha) with those reported by Barrientos and Cuéllar (2004) for *T. matacus* inhabiting areas of the Bolivian Chaco (14 ha) is not useful, as those authors used a modified MCP estimate where they considered only nonoverlapping areas as an animal's home range. On the other hand, the MCP estimates for *T. matacus* obtained here were similar to those obtained for its only congener in Northeast Brazil.

For such a small body mass (1.1–1.5 kg), *Tolypeutes* presents a relatively large home range area when compared to armadillos from other subfamilies with more generalist feeding habits, such as the small *Chaetophractus vellerosus* (0.7 kg,  $0.72 \pm 1.3$  ha—Pagnutti et al. 2014) and the heavier *E. sexcinctus* (4.4 kg,  $17 \pm 23$  ha—Medri 2008) and *D. novemcinctus* (3.2–4.4 kg, 2–20 ha—Eisenberg and Redford 1999; Loughry and McDonough 2013b). McDonough and Loughry (2008) suggested that species that rely heavily on ants and termites, such as those of the subfamily Tolypeutinae (i.e., *Tolypeutes* spp., *Cabassous* spp., and *P. maximus*), tend to have large, dispersed home ranges and few social interactions. This resembles the pattern observed here and those recently reported for other myrmecophagous such as *Cabassous unicinctus* (1.7 kg, 380 ha—Desbiez et al. 2018) and *P. maximus* (33 kg, 1,946 ha—Desbiez et al. 2020). As for other mammal orders (Tucker et al. 2014), diet seems to be an important factor to determine home range scaling in relation to body mass for armadillos. Furthermore, insectivores that rely on sparsely distributed resources have, like carnivores (Carbone et al. 2007), larger home ranges when compared to omnivores.

Home range size and overlap patterns among males and females of a population can be used to infer social mating system

of a species (Clutton-Brock 1989). In this study, females had smaller, nonoverlapping home ranges and males larger ranges overlapping with both males and females. Each male overlapped the home range of at least two females, and one tracked male was able to overlap the home range of six females, almost all the monitored females in an area. Meanwhile, females' home ranges were overlapped by up to five male individuals. Considering this space use pattern, characterizing the mating system of *T. matacus* depends on whether males are capable, or willing, to protect receptive females from other males. If males protect receptive females, the system can be described as polygynous. In this mating system, males may mate with the same group of females in successive mating events (Clutton-Brock 1989). However, if receptive females are not protected by a male, given the exposure of females to multiple males, promiscuity cannot be excluded as a possibility both for males and females (Clutton-Brock et al. 1989). In a promiscuous social mating system males and females may mate with multiple partners, with no continuing bond between the mating individuals (Clutton-Brock 1989). There is an abundance of examples of evolutionary forces that can lead small mammal females to promiscuity: e.g., to induce sperm competition (Keil and Sachser 1998); guarding against male infertility (Wolff and Macdonald 2004); paternity confusion and prevention of infanticide (Agrell et al. 1998); or simply as the result of sexual harassment (Wolff and Macdonald 2004).

The sexual dimorphism observed in *T. matacus* (with larger males) is one indication of a polygynous mating system, as different selection pressures on males and females can generate more pronounced sexual dimorphism in the body size (Clutton-Brock et al. 1989; Heske and Ostfeld 1990). Other armadillos have been characterized as polygynous (*D. novemcinctus*—McDonough 2000), polygynous or promiscuous (*P. maximus*—Desbiez et al. 2020), or promiscuous (*C. vellerosus*—Nardelli et al. 2020). Although other xenarthrans, such as sloths, also have been recorded to exhibit a polygynous mating behavior (e.g., *Bradypus variegatus*—Pauli and Peery 2012), long-term space use and genetic studies have shown that females of *B. variegatus* and *Choloepus hoffmanni* commonly mate with more than one male, characterizing a promiscuous behavior (Garcés-Restrepo et al. 2017).

For many terrestrial mammal species, female spacing typically is dictated by resource abundance and distribution (Sandell 1989). Darwinian fitness for females is acquired by successfully raising their young (Main et al. 1996) and the smaller and almost exclusive ranges occupied by the females in our study should guarantee enough resources for them and their offspring. Furthermore, small home ranges, relative to the species' potential mobility, may contribute to the protection of offspring against predators and infanticide (Emlen et al. 1989; Agrell et al. 1998).

Male three-banded armadillos seem to be nonterritorial, which can occur when females are solitary and unpredictably distributed. Instead of guarding a territory, dominant promiscuous or polygynous males tend to increase their chances of reproductive success by actively searching for females

(Clutton-Brock 1989). Because *T. matacus* is not a seasonal breeder, receptive females can be distributed in an unpredictable manner across space and time, and males can try to increase their chance of encountering receptive females by covering areas larger than those defined strictly by their energetic requirements (Sandell 1989). We captured several females at different gestational stages in both summer and wintertime (Attias 2017), which indicates reproductive activity during our study period and no apparent seasonality.

Daily distance traveled scaled with home range size, and male home range size scaled with body mass, i.e., larger males had higher daily ranges. Larger males therefore can afford, energetically, to range over larger areas (McNab 1963) and increase their chances of encountering females in estrus. In a long-term monitoring project with *D. novemcinctus*, McDonough (2000) reported that females tend to pair with males with high overlap of their home range. Thus, reproductive success of three-banded armadillo males could be associated with body mass, because these individuals have larger home ranges and higher daily distances traveled, potentially encountering more females.

Males of *T. tricinatus* also exhibited home range areas ( $238 \pm 103$  ha) an order of magnitude larger than those of adult females ( $24 \pm 12$  ha—Guimarães 1997). These similarities with the spatial patterns reported by Guimarães (1997) for *T. tricinatus*, where males are heavier, home ranges scale with body mass, and males exhibit larger home ranges than females, indicate that both *Tolypeutes* species might share a similar mating system. Nevertheless, chasing behavior, where several males pursue a single female presumably in estrus, has been reported for *T. tricinatus* (Bernier 2003; Bocchiglieri et al. 2010; Marini-Filho and Guimarães 2010) but to date has not been observed for *T. matacus*.

The spacing patterns observed for individuals of both sexes were related to age class and activity status of individuals and reinforce the sociobiological aspects found for other armadillo species, which are characterized as solitary, asocial mammals, with rare social interactions mostly related to breeding behavior (McDonough 2000; Loughry and McDonough 2013b; Loughry et al. 2015; Desbiez et al. 2020). The higher intersexual probability of overlap when compared to the intrasexual reinforces the breeding-related aspects of the rare social interactions between *T. matacus* individuals. The lower probability of core area sharing can be related to the fact that burrow sharing between adult *T. matacus* is not common and only has been recorded on rare occasions of extreme cold and in a temporary manner (Meritt 2008). Individuals of different age classes presented higher probabilities of space use sharing, regardless of their activity status, when compared to same age pairs. This can be explained at least partially by the fact that females tend to share their shelters, and consequently their home range, with their young (Attias et al. 2016). Interestingly, adult females do not tend to tolerate any space use sharing with other females, not even nonreproductive juveniles, with the exception of juvenile females that were still being nursed by their mothers, and had their home range almost completely

encompassed by their mother's home range. Even dispersing subadult females seem to avoid extensive space use sharing with other females (Attias 2017).

This study was not designed to compare human-modified to conserved areas; however, it bears noting that we did not find differences in basic ecological characteristics (e.g., home ranges size, overlap, and activity patterns) between the individuals monitored in the preserved flooded savanna areas and those monitored in pasturelands. Nevertheless, future studies should address more directly how this species can be affected by habitat modification to enable proper, species-specific conservation planning. Habitat destruction for agricultural and ranching activities is common throughout the species' distribution (Jarvis et al. 2010). Studies focusing on individual responses to land management practices in these types of land use (e.g., prescribed fire) and on the population's health and persistence in these landscapes therefore can contribute to the species' conservation.

Although we monitored animals for a relatively short period, our intensive monitoring methods allowed us to characterize the basic aspects of this species' ecology and make valuable inferences on its social biology. We characterize three-banded armadillos as a primarily nocturnal species with home range and spacing patterns that point to a generally asocial behavior and a polygynous or promiscuous mating system. While the IUCN classifies the southern three-banded armadillo as "Near Threatened," citing vulnerability to harvest and habitat destruction, it is classified as "Data Deficient" by the Brazilian authorities. We hope that the basic ecological results reported here will be able to guide future research efforts in support of this species' conservation in Brazil.

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## SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Detailed information on the individuals of *Tolypeutes matacus* monitored at two sites in the Pantanal of Brazil, from November 2014 until August 2015.

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