



Spatial ecology of the giant armadillo *Priodontes maximus* in Midwestern Brazil

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The giant armadillo (*Priodontes maximus*) is the largest living armadillo. This naturally rare and poorly known species is endemic to South America and classified as “Vulnerable” by the IUCN. Here we explored aspects of the spatial ecology of *P. maximus* in Midwestern Brazil to gain insights on its ecology and biology to support conservation efforts. In 8 years, we identified 50 individuals of *P. maximus* and monitored 23 of them using telemetry methods. To characterize site fidelity and home range, we fitted individual continuous-time movement models and estimated Autocorrelated Kernel Density Estimates. We built a Structural Equation Model to evaluate how home-range area and daily displacement are related to each other, to sampling effort, and to individual characteristics. We estimated home-range overlap between pairs of different sexes using a bias-corrected Bhattacharyya coefficient. Finally, we formulated a canonical density estimation formula to characterize minimum population density. We gathered a total of 12,168 locations of *P. maximus*. The best-fitted movement models indicated site fidelity for all individuals and a median adult home-range area of 2,518 ha. Median adult daily displacement was 1,651 m. Home-range area scales positively with daily displacement and daily displacement scales positively with body mass. Median home-range overlap between pairs was low (4%) and adult females presented exclusive home ranges among themselves. Median minimum density was 7.65 individuals per 100 km² ($CI = 5.68\text{--}10.19$ ind/100 km²). Our results are congruent with characterizing *P. maximus* as a generally asocial species, most likely promiscuous/polygynous, that establishes large, long-term home ranges, which grants the population a naturally low density. Spatial patterns and biological characteristics obtained in this study can be used to guide future conservation strategies for *P. maximus* in the Pantanal wetlands and elsewhere.

Key words: autocorrelated kernel density estimates, Cingulata, conservation, home range, minimum density, Pantanal, site fidelity, static interaction, telemetry, Xenarthra

O tatu-canastra (*Priodontes maximus*) é o maior tatu vivente. Esta espécie naturalmente rara e pouco conhecida é endêmica da América do Sul e é classificada como “Vulnerável” (UICN). Aqui exploramos aspectos da ecologia espacial de *P. maximus* no centro-oeste brasileiro para obter insights sobre sua ecologia e biologia a fim de apoiar esforços de conservação. Em oito anos, nós identificamos 50 indivíduos de *P. maximus* e monitoramos 23 deles utilizando métodos de telemetria. Para caracterizar a fidelidade territorial e o tamanho da área de vida,

ajustamos modelos individuais de movimento em tempo contínuo e estimamos modelos de densidade de Kernel para dados autocorrelacionados. Nós construímos um Modelo de Equação Estrutural para avaliar como a área de vida e o deslocamento diário estão relacionados entre si, ao esforço amostral, e as características individuais. Nós estimamos a sobreposição da área de vida entre pares de diferentes sexos usando o coeficiente de Bhattacharyya com viés corrigido. Finalmente, criamos uma fórmula para estimativa canônica de densidade a fim de caracterizar a densidade mínima da população. Reunimos um total de 12 168 localizações de *P. maximus*. Os modelos de movimento com o melhor ajuste indicaram fidelidade territorial para todos os indivíduos e uma área de vida mediana de 2 518 ha para adultos. O deslocamento diário mediano dos adultos foi de 1 651 m. A área de vida está positivamente relacionada com o deslocamento diário e o deslocamento diário está positivamente relacionado com a massa corporal. A sobreposição mediana da área de vida entre pares foi baixa (4%) e fêmeas adultas apresentaram áreas de vida exclusivas entre si. A mediana da densidade mínima foi de 7,65 indivíduos por 100 km² (IC = 5,68 – 10,19 ind/100 km²). Através deste estudo, foi possível caracterizar *P. maximus* como uma espécie, em geral, não-social, provavelmente promíscua/polígama, que estabelece grandes áreas de vida por longos períodos, o que confere à população uma densidade naturalmente baixa. Padrões espaciais e características biológicas, como as obtidas neste estudo, devem ser utilizadas para guiar futuras estratégias de conservação para *P. maximus* no Pantanal e em outros locais.

Palavras-chave: Estimativas de densidade de Kernel para dados autocorrelacionados, Cingulata, conservação, área de vida, densidade mínima, Pantanal, fidelidade territorial, interação estática, telemetria, Xenarthra.

The giant armadillo (*Priodontes maximus* Kerr, 1792) is by far the largest species of extant armadillos (Cingulata: Chlamyphoridae—Emmons and Feer 1997) with a body mass between 28 and 50 kg and a total length that can reach up to 150 cm (Emmons and Feer 1997; Nowak 1999; Carter et al. 2016; Desbiez et al. 2019). *Priodontes maximus* is a long-living (12–15 years—Nowak 1999), myrmecophagous species, feeding mainly on ants and termites (Anacleto 1997; Anacleto and Marinho-Filho 2001; Anacleto 2007), whose few predators are large carnivores such as jaguars (*Panthera onca*) and pumas (*Puma concolor*—Nowak 1999). Individuals of the species play an important role as ecosystem engineers, building large burrows that are used by several vertebrate and invertebrate species (Leite-Pitman 2004; Desbiez and Kluyber 2013; Aya-Cuero et al. 2017; Massocato and Desbiez 2017). These animals are found at low density over much of South America east of the Andes: Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, and Venezuela, in habitats ranging from tropical forest to open savanna (Smith 2007; Abba and Superina 2010). In Brazil, this species can be found in the Amazon, Atlantic Forest, Cerrado, and Pantanal ecoregions (Fonseca et al. 1996). Although regionally widespread, *P. maximus* are locally rare (Meritt 2006) and are threatened by habitat loss and fragmentation, hunting activities, road collisions, and suspected illegal traffic (Anacleto et al. 2014; Chiarello et al. 2015; Carter et al. 2016). The species is currently classified as “Vulnerable,” by the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species (Anacleto et al. 2014), and by the Brazilian Institute for Biodiversity Conservation (ICMBio—Chiarello et al. 2015), due to a population decline of more than 50% over the last three generations caused by habitat loss and exploitation.

Similar to most armadillo species, due to their solitary, nocturnal, and fossorial habits, *P. maximus* are rarely seen and are considered difficult to capture and study in the wild (Eisenberg and Redford 1999; Noss et al. 2004; Silveira et al. 2009; Superina et al. 2014b; West et al. 2014; Quiroga et al.

2017). Overall, researchers have rarely attempted the capture of *P. maximus*, and only a small number of individuals have been captured in previous studies (e.g., Carter and Encarnação 1983; Encarnação 1986; Anacleto 1997; Leite-Pitman et al. 2004; Silveira et al. 2009). Animals have been reported to occupy home ranges between 300 and 1,500 ha (Carter and Encarnação 1983; Noss et al. 2004) with little overlap among individuals (Silveira et al. 2009). However, these small data sets have limited potential to provide information on the species and many gaps remain regarding their population biology. This lack of reliable basic biological information can hinder conservation efforts (Greene 2005; Beyer et al. 2010; Superina et al. 2014b).

The use of spatial ecology can be particularly helpful to study recondite species such as this one, with well-developed burrowing habits, providing information on their biological characteristics (e.g., bioenergetic strategies, feeding behavior, social behavior and, reproductive strategies), and ecological functions that cannot be easily assessed through direct observation (Clutton-Brock et al. 1989; White and Garrot 1990; Millsbaugh and Marzluff 2001; Cagnacci et al. 2010; Attias 2017). Movement patterns are the spatial expression of the strategies species adopt to survive and reproduce (Burt 1943). Understanding animal space use can be key to developing effective population management and conservation strategies (Collinge 2001). Here we aim to explore aspects of the spatial ecology of the giant armadillo, *Priodontes maximus*, in Midwestern Brazil to gain insights into its ecology and biology to support conservation efforts. To accomplish this, we studied movement patterns of *P. maximus* at varied spatial and temporal scales, ranging from daily distances traveled to pluri-annual home-range areas, evaluating site fidelity, home-range overlap, and minimum population density.

MATERIALS AND METHODS

The Giant Armadillo Conservation Program (GACP) was set up in July 2010 as a long-term study that uses a broad array of approaches to study the biology and ecology of *P. maximus* (www.gacp.org.br).

giantarmadillo.org). The main goal of the GACP is to investigate the natural history and biology of *P. maximus* and use field data to inform conservation decision making and outreach programs. This study was performed under License No. 27587 from the Chico Mendes Institute for Biodiversity Conservation, granting permission to capture, immobilize, and manipulate armadillos, and collect and store biological samples. All procedures followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016).

Study area.—This study was carried out between July 2010 and January 2018, in a 350-km² area that includes 10 extensively managed cattle ranches (19°16'60"S, 55°42'60"W) in the Brazilian Pantanal (Nhecolândia subregion). The landscape is a mosaic of different habitats that include open grassland, scrub grassland, scrub forest, and semi-deciduous forest (Fig. 1). Historical mean temperature is 25.4°C, climate is classified as semi-humid tropical (Aw), with a hot, rainy season (October to March), and a warm drier season (April to September) during which temperatures may drop due to cold fronts from the South

(Soriano 2000). The area lacks watercourses but there is widespread flooding during the rainy season and permanent lakes. Traditional extensive cattle ranching is practiced in the area and, overall, anthropogenic threats are low.

Capture, handling, and monitoring.—We performed active searches by foot or pickup trucks looking for signs (tracks, feces, and burrows) of *P. maximus*. Animals were captured using traps that were placed at the entrance of burrows with evidence of recent activity (following Carter 1985; Silveira et al. 2009; West et al. 2014). Traps consisted of cylindrical iron cages with a trap door that was triggered upon entry. Traps had a diameter similar to that of the burrow entrance and a length of 2 m. Once captured, animals were temporarily placed in ventilated wooden boxes (Superina et al. 2014a) reinforced with metal sheeting, then anesthetized by intramuscular injection in the hind limbs. The anesthetic was composed of Butorphanol 10 mg/ml (0.1 mg/kg), Detomidine 10 mg/ml (0.1 mg/kg), Midazolam 5 mg/ml (0.2 mg/kg), and Ketamine hydrochloride (10 mg/kg—Kluyber 2016). Once immobilized,

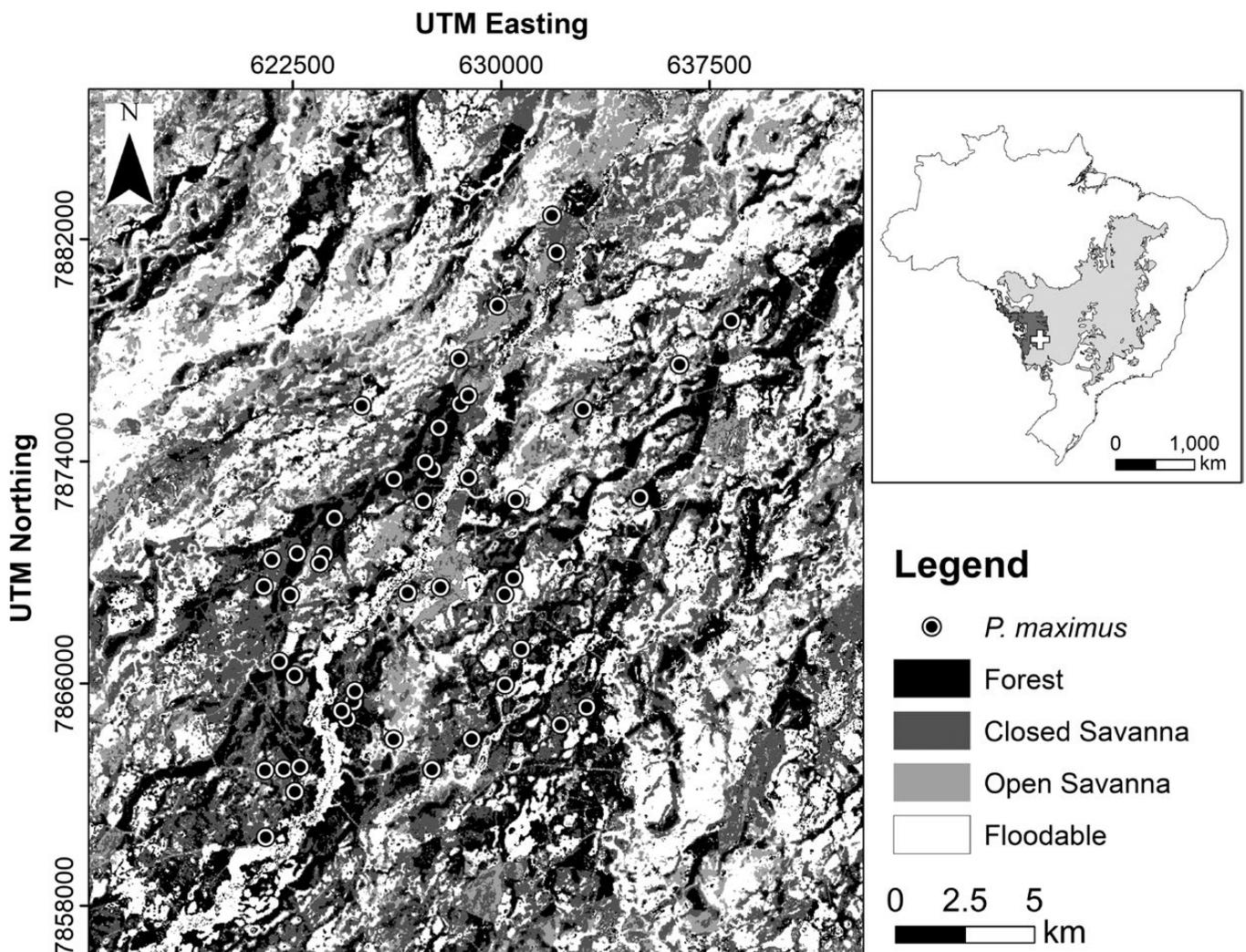


Fig. 1.—Landscape structure of the study site and central locations of each one of the 50 giant armadillos (*Priodontes maximus*) detected in the Baía das Pedras ranch between October 2011 and January 2018. In the upper right, the location of our study site (white cross), in the Pantanal region (dark gray), and the neighboring Cerrado region (light gray), Brazil.

we collected information on age, sex, body mass, morphological measurements, and any natural marks that could allow further individual identification (Desbiez et al. 2019). We defined subadults as prepubescent individuals with no signs of sexual activity (Desbiez et al. 2019). Subadult females present smaller vulvar diameter and poorly developed teats when compared to sexually active adults, whereas subadult males present azoospermatic ejaculation and relatively shorter penis length when compared to sexually active adults (Desbiez et al. 2019).

Armadillos were implanted with intra-abdominal VHF radio transmitters (Silveira et al. 2009) following the surgical procedures proposed by Hernandez et al. (2010). Transmitter weights were 38.5 g, i.e., ca. 1.3% of armadillo's body mass (IMP 310, Telonics, Inc., Mesa, Arizona). Most animals were also temporarily fitted with a GPS tracking device at the moment of first capture and/or through recaptures during its long-term VHF monitoring. GPS devices weighed 71 g, i.e., 2.4% of armadillo's body weight (TGW-4100-2, Telonics, Inc., Mesa, Arizona) and were externally attached to the animal's carapace, while anesthetized, following methods previously used by Silveira et al. (2009). Devices were programmed to obtain fixes with 30 min intervals between 1800 h and 0400 h, the animal's activity period according to preliminary camera trap records. Once all procedures were terminated, anesthesia was reversed through an intravenous injection of Naloxone (0.04 mg/kg), Yohimbine (0.125 mg/kg), and Flumazenil (0.025 mg/kg—Kluyber 2016). After full recovery in a ventilated wooden box, animals were released in the same burrow from which they were captured, less than 24 h after initial capture. To record burrow locations, animals were monitored during daytime for an average of 15 days per month, by means of VHF telemetry, using the homing-in to the animal technique (Samuel and Fuller 1994). Cameras were usually left between 30 and 60 days to document the animal's health, visitors to the burrow, and potential transient animals. GPS devices were recovered for data download once they fell off the animal.

Home range, site fidelity, and daily displacement.—We used three different methods to estimate the home range of *P. maximus*. To allow comparisons of our results with previous studies (Carter and Encarnação 1983; Noss et al. 2004; Silveira et al. 2009), we generated home-range area estimates using the Minimum Convex Polygon (MCP) method, a simple estimator that consists of connecting the most external records forming the smallest polygon without concavities (Mohr 1947). We also used Kernel probabilistic nonparametric models (KDE—Worton 1987), which are considered more appropriate to Kernohan et al.'s (2001) definition of home range, given that the model considers the use of space in a probabilistic and continuous way (Millsbaugh et al. 2006). 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). KDE was estimated using the same grid for all individuals (grid resolution = 400) and a bivariate normal distribution for each kernel. The fixed smoothing parameter ($h = 310$) was estimated as the median value of the normal reference rule values (h -ref—Worton 1995) obtained for each individual. All the above-mentioned analyses were performed using the R package “adehabitatHR” (Calenge 2006; R Development

Core Team 2018). Despite the broad application of KDE in home-range estimation, it overlooks the temporal and spatial autocorrelation structure of GPS data sampled at high temporal frequencies. If location data are not independent and identically distributed, KDE can generate biased home-range estimates (Fleming et al. 2015; Fleming and Calabrese 2017).

Autocorrelated Kernel Density Estimates (AKDE—Fleming et al. 2015) is an efficient nonparametric home-range estimator for animal tracking data, producing more accurate home-range area estimates, particularly with small sample sizes (Fleming and Calabrese 2017; Noonan et al. 2019). We used the R package “ctmm” (Fleming and Calabrese 2018) for variogram estimation, movement model selection and fitting, and AKDE estimation. To incorporate GPS error into the analysis, we calibrated error from the Horizontal Dilution of Precision (HDOP) values of a stationary GPS device (error = 9.5 m). To visually inspect the autocorrelation structure of the location data of each animal, we plotted the estimated semivariance as a function of time lag (Calabrese et al. 2016). We estimated continuous-time movement models for each individual data set based on patterns of temporal and velocity autocorrelation of the movement data. At zero to short time lags, a linear increase in the semivariance corresponds to uncorrelated velocity, suggesting movement models such as Brownian motion (BM; random, undirected movement) or Ornstein-Uhlenbeck (OU; Brownian Motion within a home range). Upward curvature at these time lags indicates velocity autocorrelation and suggests movement models such as OU with foraging (OUF; assumes regular BM while foraging, on a very short time scale, and OU on longer time scales—Fleming et al. 2014). Models were fitted via maximum likelihood and selected using Akaike's Information Criterion (AIC; see Supplementary Data SD1 for selected model parameters). Finally, home-range areas were estimated using the fitted selected model for each individual (Calabrese et al. 2016). AKDE home-range area estimates are characterized by a maximum likelihood value followed by the lower and upper limits of a 95% confidence interval.

We also used the selected model for each individual to make inferences regarding range-residency and site fidelity (Calabrese et al. 2016; Winner et al. 2018). Animals that do not establish a home range should have their tracking data best fitted to a BM movement model, which portrays a random search in an area of infinite extent, since relocation velocities are uncorrelated and positions are unconstrained. Animals that establish a home range and present site fidelity can portray either an OU or an OUF movement mode. These movement models indicate that the animal tends to perform random search around a location, showing a tendency to stay in this location's vicinity; i.e., site fidelity (Fleming et al. 2014).

To estimate daily distance traveled by individuals, we excluded the top 1% of steps with the highest velocities that are commonly associated with GPS reception failures, generating abnormally large steps. The daily distance traveled was then estimated as the cumulative sum of all step lengths given in a 24-h period by an individual. Due to the nocturnal activity behavior of *P. maximus*, we estimated the distance moved between midday of 1 day until 1159 h of the next day as the daily distance moved. Daily distance moved by each individual was

characterized as the median of the distances traveled each day they left their burrow for activity during their monitoring period.

We built a Structural Equation Model (SEM—Grace 2006) to evaluate the relationship between home-range area, daily displacement, sampling effort, sex, and body mass of individuals. SEM allows for simultaneous estimation of covariation between multiple variables in a single model, and allows the specification of multiple predictive pathways between model variables to account for their influence on each other (Grace 2006; Crouch and Mason-Gamer 2018). We built a model to evaluate how home-range area (AKDE 95%) and daily displacement are related to each other, sampling effort (number of GPS and VHF locations and, number of days of monitoring through both methods), individual's body mass, and sex. Larger individuals could occupy larger areas and move more. This could be either because these individuals need more energetic resources and need to range over larger areas to find them, or because of their potentially larger energetic storage, which allows them to cover larger areas (Jetz et al. 2004; Nathan et al. 2008). In addition, different evolutionary selective pressures on males and females could result in different forms of space use between sexes (Clutton-Brock et al. 1989). Hence, larger animals can potentially move farther distances, covering large areas or not, depending on internal and external motivations (Jetz et al. 2004; Nathan et al. 2008). To build and test the SEM, we used the packages “lava” (Holst and Budtz-Joergensen 2013) and “piecewiseSEM” (Lefcheck 2016) in the R platform.

Home-range overlap.—We estimated the home-range overlap (i.e., static interaction) between pairs of individuals of different sexes. To characterize the similarity between two probability distributions (i.e., AKDE home-range estimates) we estimated a bias-corrected Bhattacharyya coefficient with confidence intervals using the R package “ctmm” (Bhattacharyya 1943; Fleming and Calabrese 2018; Winner et al. 2018). This coefficient can range from 0 (no overlap) to 1 (overlap with identical distributions), and is considered the most appropriate measure for quantifying the degree of similarity among utilization distribution estimates (Fieberg and Kochanny 2005; Winner et al. 2018). Overlap coefficients are represented by a Maximum Likelihood (ML) value and the correspondent confidence interval (CI). To estimate the median values of overlap for each sex we used only overlap values of neighboring animals (i.e., those for which the outermost locations of each animal are < 2 km apart). Pairs of animals that are more than 2 km apart are unlikely to interact unless one of the individuals leaves its area of occupancy for exploratory activities or changes its territory. We fitted a Linear Mixed Effects model (LME) to evaluate the fixed effect of the sex of individuals in a pair (i.e., Male–Male, Male–Female, or Female–Female) on the ML values of the overlap coefficient, considering the random nested effect of individuals identity, which accounts for the potential autocorrelation structure between overlap values obtained for the same individual. Model fit was implemented using the R package “nlme” (Pinheiro et al. 2018).

Minimum density estimation.—Minimum population density was estimated using a subset of our study area where we were confident that we tracked all resident individuals (Fig. 2). We

detected other, possibly transient, individuals using camera trap methods. Camera traps were installed in front of the entrance of burrows used by monitored animals (6,309 camera trap/nights) and also were set in a grid configuration within areas known to be used by monitored armadillos in this section of the study area (4,500 camera trap/nights; Fig. 2). Only one camera was set at each sampling point. Cameras were set for an average of 40 consecutive days and were active 24 h a day. Camera traps enabled the detection of captured armadillos, resident armadillos that had not yet been captured, and transient armadillos. *Priodontes maximus* individuals were identified through variations in scale coloring pattern, such as the number and arrangement of light and dark scales in the carapace and tail (Noss et al. 2004), and other natural marks such as scars.

To estimate *P. maximus* density, we started from the canonical density estimation formula as follows: $D = N/A$; where D is density; N , the number of individuals in the sampled population; and A , the effective sampled area (Soisalo and Cavalcanti 2006). We used a conservative approach and based N only on the known resident individuals excluding transient animals. If animals present zero home-range overlap (O) and do not present absence gaps throughout their spatial distribution, the effective sampled area (A) could be roughly approached by multiplying N by species home-range size (H). Otherwise, if overlap occurs without gaps, effective sampled area (A) should be smaller than the former estimation ($N * H$), and in this case should account with home-range overlapping (O) as follows $A = N * (H - (H * O))$. Then we estimated giant armadillo density by solving $D = N/N * (H - (H * O))$.

To incorporate the uncertainty of our observations on density estimation and obtain 95% CIs of the estimation, we applied a bootstrapping procedure while solving the proposed density estimation formula above. Because we have uncertainty in each parameter (N , H , and O) that composes the density formula, we ran the formula 50,000 times, sampling values from the original parameters' distribution with replacement. For each run, sampled parameters values were averaged to solve the density formula (see Supplementary Data SD2 for the R code used in this analyses). Expected density estimation and lower and upper 95% CI were calculated using, respectively, the median, 2.5%, and 97.5%, quantiles of the 50,000 density values estimated in bootstrapping.

RESULTS

Over a period of 8 years, we identified 50 *P. maximus* within the study area, 28 females, 21 males, and 1 individual of unidentified sex (Fig. 1). Of these, 21 individuals were detected exclusively through camera traps (see Supplementary Data SD3), while 29 (15 M; 14 F) were captured (Supplementary Data SD4). Of the latter, 23 were monitored through telemetry methods: some individuals escaped from the traps, while others, captured in the beginning of the study, were fitted with telemetry devices that failed. The monitoring of each animal, regardless of the tracking method applied, encompassed a mean time span of 596 ± 545 days (min = 34, max = 1,862). During this period, animals were intensively monitored by GPS telemetry

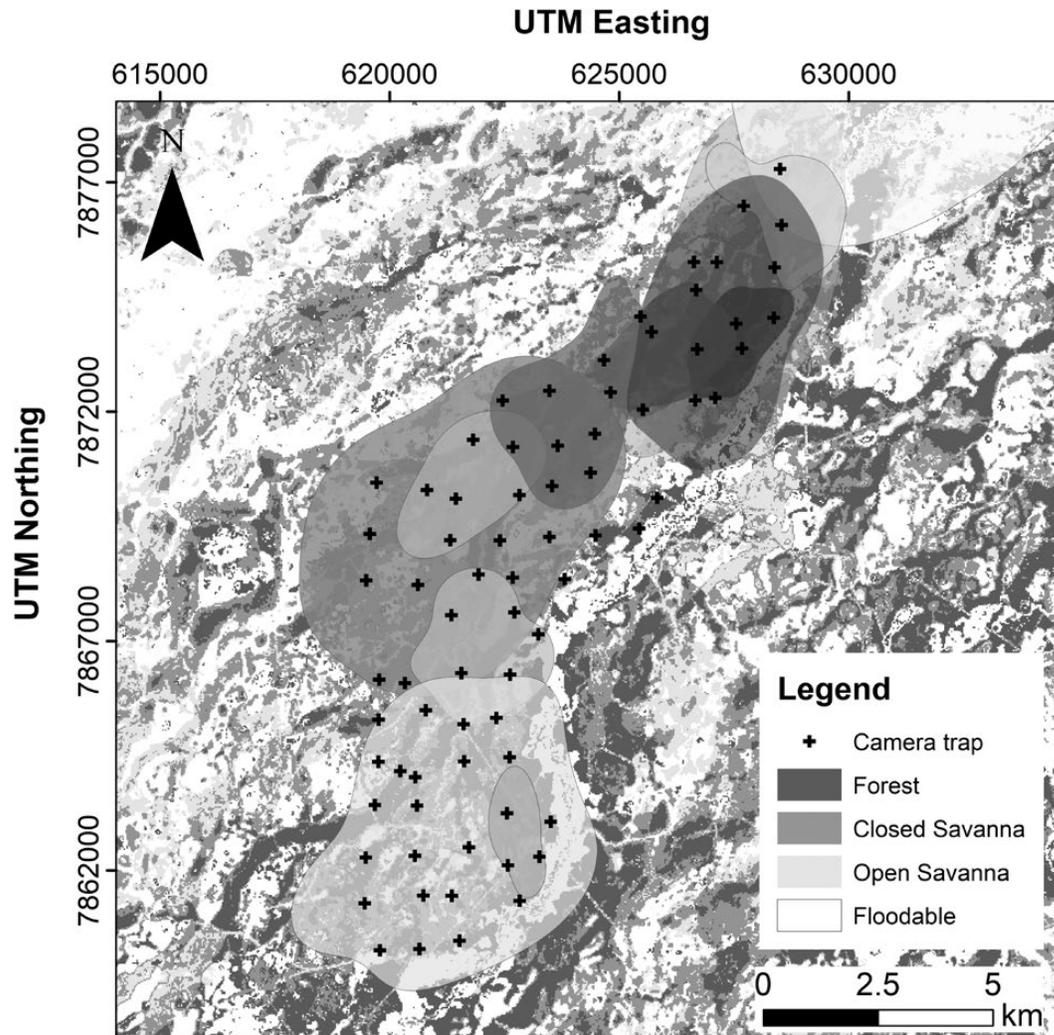


Fig. 2.—Camera trap grid set within the subset of our study area where we believe all resident giant armadillos (*Priodontes maximus*) have been tracked. Crosses represent the location of cameras along the grid. Polygons of different colors represent the maximum likelihood AKDE home-range contour for each of the 12 resident individuals tracked via telemetry at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

for an average of 70 ± 38 days (min = 21, max = 146). We gathered a mean of 505 ± 345 locations per individual (min = 66, max = 1,328) by GPS telemetry, and a mean of 44 ± 49 locations per individual (min = 2, max = 229) by VHF telemetry. We recorded a mean of 548 ± 361 locations per animal (min = 92, max = 1,402) and a total of 12,168 locations of 23 *P. maximus* individuals, using the combination of these tracking methods (Fig. 3a).

Home range, site fidelity, and daily displacement.—We estimated home-range metrics using the GPS and VHF data gathered during the study period (Supplementary Data SD4). Using a Minimum Convex Polygon (MCP 100%) approach and all gathered locations, we estimated a median home-range area of 1,946 ha (min = 284, max = 8,255) for the adult *P. maximus*, since data did not present a normal distribution. When using Kernel probabilistic nonparametric models (KDE 95%) we estimated a median home-range size of 1,731 ha (min = 477, max = 5,507) and a median

core area (KDE 50%) of 334 ha (min = 115, max = 1,161) for adult *P. maximus*. When using AKDE 95%, we estimated median home-range size of 2,518 ha for adults (95% CI = 1,817–3,063; Fig. 3b), with males occupying median ranges of 5,109 ha (CI = 3,149–7,548) and females 1,998 ha (CI = 1,642–2,389). The best-fitted movement models indicated site fidelity for all individuals (Supplementary Data SD4). Adult daily displacement ranged between 1,153 and 2,570 m, with a median of 1,651 m (Table 1). Subadults weighed on average 25.6 kg, used smaller areas (AKDE 95% = 674 ha, CI = 512–859; $t = 2.26$, $d.f. = 14.57$, $P = 0.03$) and travelled shorter distances daily (range = 410–1,668 m, $Med = 1,274$ m; $t = 2.47$, $d.f. = 14.21$, $P = 0.03$; Table 1; Supplementary Data SD4), when compared to adults.

Our SEM presented an adequate model fit to observed data ($X^2 = 0.63$, $d.f. = 5$, $P = 0.99$). Home-range area was not related to sampling effort (but see Supplementary Data SD5 for SEM results when using KDE estimates). The SEM results show that

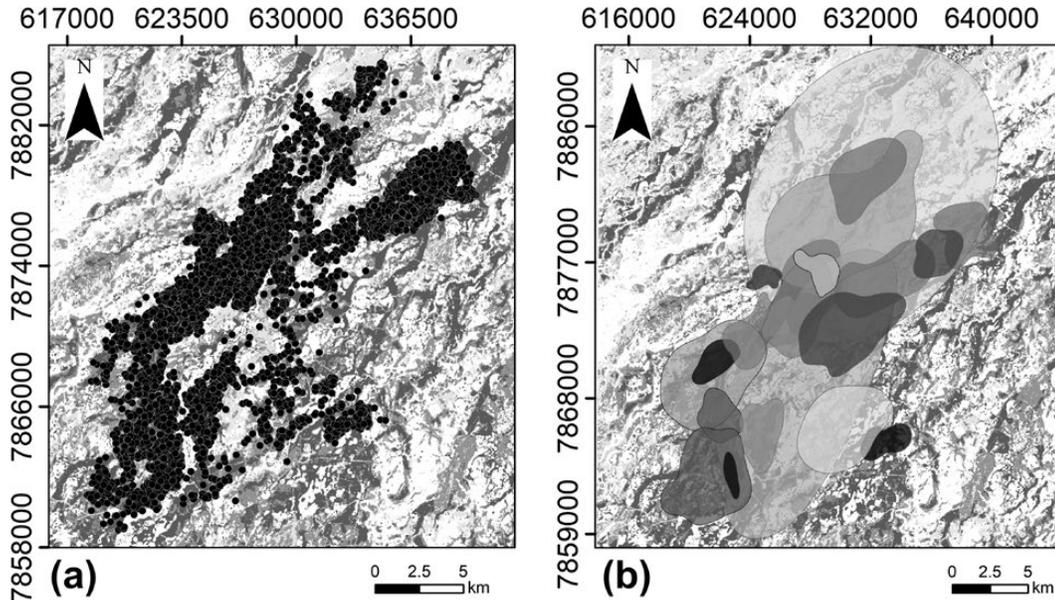


Fig. 3.—Telemetry locations (a) and maximum likelihood home-range contour (AKDE; b) of each of the 23 *Priodontes maximus* tracked at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

Table 1.—Summary estimates for 23 individuals of *Priodontes maximus* captured at Baía das Pedras ranch, Corumbá, Brazil, from October 2011 until January 2018. Data on adult (F = 9, M = 6) and subadult (F = 4, M = 4) individuals are presented using median (minimum–maximum) values, of: Body mass (kg); Total monitoring time span (days), with VHF or GPS telemetry; Number of locations obtained through GPS and VHF telemetry together; estimates of home range—Minimum Convex Polygon (MCP 100%); Kernel Density Estimate (KDE 95%); core area estimates (KDE 50%); Autocorrelated Kernel Density Estimates (AKDE 95%); and mean daily displacement (m). Home-range estimates are given in hectares. A more comprehensive analysis of sexual dimorphism in morphological characters was presented in [Desbiez et al. \(2019\)](#).

	Adult		Subadult	
	Female	Male	Female	Male
Body mass	32 (28.6–36)	35.75 (31.4–36.9)	26.1 (18–28.3)	27.6 (20.6–30.4)
Total monitoring period	589 (93–1,862)	263 (22–1,011)	430 (333–487)	497 (34–1,178)
Number of locations	475 (92–1,402)	313 (64–999)	366 (263–942)	465 (182–955)
MCP 100%	1,272 (284–2,947)	3,049 (851–8,255)	516 (385–853)	546 (192–1,247)
KDE 95%	1,508 (477–2,519)	2,125 (967–5,507)	714 (573–975)	760 (430–1,257)
KDE 50%	318 (115–645)	394 (119–1,162)	181 (127–259)	207 (80–350)
AKDE 95%	1,998 (274–2,742)	5,109 (1825–22,198)	722 (428–2,178)	652 (229–1,267)
Daily displacement	1,651 (1,153–2,115)	1,636 (1,287–2,570)	1,239 (1,005–1,623)	1,452 (410–1,668)

home-range area scaled positively with daily displacement and daily displacement scaled positively with body mass ([Fig. 4](#); [Supplementary Data SD6](#)). Accordingly, the effect of body mass on home range is given through its influence over daily displacement. Daily displacement did not differ between sexes, although home-range size did. Males and females of similar body mass walk, therefore, the same distance daily but will range over areas of different sizes.

Home-range overlap.—Median home-range overlap between pairs of adult individuals was extremely low (0.04, $CI = 0.01–0.14$; [Fig. 3b](#)). The amount of overlap between individuals differed according to the sex of the individuals of the pair. Female–Female pairs presented lower overlap values when compared to Male–Female pairs ($t = -2.80$, $P = 0.01$; [Table 2](#)). In contrast, the overlap between Male–Male pairs did not differ from Male–Female pairs ($t = 0.54$; $P = 0.58$). Adult females did not overlap home ranges of other adult

females, as such presenting exclusive home ranges. Females also presented low overlap with adult males, whereas Male–Male pairs presented the highest observed overlap values ([Table 2](#)).

Minimum density estimation.—During the 8 years of monitoring in the study area, we were able to detect 50 individuals of *P. maximus* (adult and subadults) that jointly occupied an area of 36,897 ha ([Fig. 1](#); [Supplementary Data SD3](#)). Nevertheless, our primary density estimates were based on a cluster of 12 individuals that were captured and monitored in an area that was intensively monitored throughout our study period ([Fig. 2](#)). In this area, the home-range edges of the individuals fit perfectly together, like a jigsaw puzzle, making us believe (due to the low overlap pattern encountered in this study and the camera trap grid records) that we sampled the majority of the individuals occupying this subset of our study area. From the 12 individuals monitored in the area, 10 were

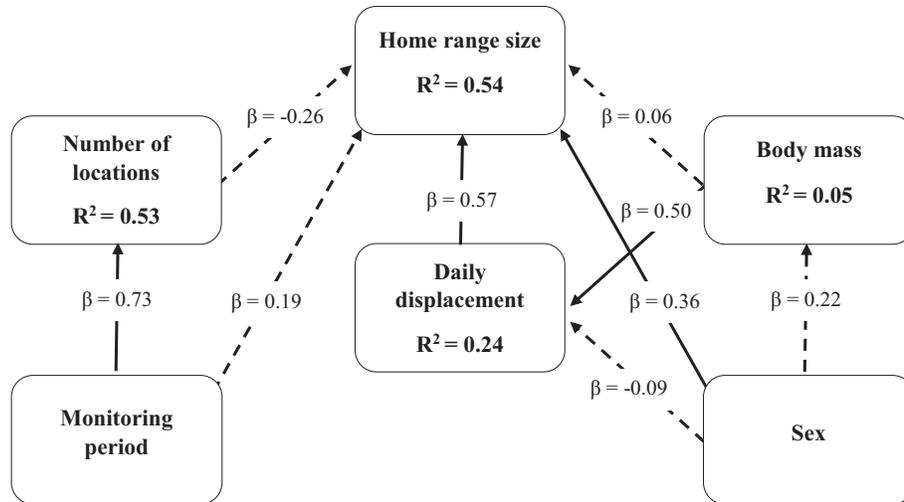


Fig. 4.—Diagram of the Structural Equation Model built to explain the relationship between individual daily displacement (m), home-range area (Autocorrelated Kernel Density Estimate), and sampling effort (represented by the number of locations gathered using GPS and VHF telemetry and by the number of monitoring days through both methods), individual body mass (kg), and sex. Arrows indicate the directional effect of one variable over another. Solid arrows indicate statistically significant relationships, whereas dashed arrows represent nonsignificant relationships tested. Values overlaying each arrow are the standardized path coefficients (β values) for each relationship. Model R^2 values are given inside the box of each dependent variable. Data from 23 *Prionotus maximus* tracked at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

Table 2.—Observed and predicted static interaction between pairs of individuals of *Prionotus maximus* according to its sex. Observed static interaction is characterized at home-range level by the median Maximum Likelihood values of a bias-corrected Bhattacharyya coefficient (and the upper and lower limits of its confidence interval). Predicted overlap values were obtained by fitting a Linear Mixed Effects Model and are characterized in the same manner. Data from 22 individuals tracked at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

Sex of individuals	Observed overlap	Estimated overlap
Female–Female	0.001 (0.00001–0.009)	0.07 (0.03–0.11)
Male–Male	0.16 (0.001–0.41)	0.17 (0.12–0.21)
Male–Female	0.09 (0.02–0.19)	0.14 (0.10–0.18)

resident and 2 occupied the area for a period and died (subadult male TC17, preyed upon by puma, *Puma concolor*) or dispersed (subadult male TC10). The joint area occupied by the 12 resident individuals in this intensively sampled subset of our study site was of 14,157 ha and was used as the area (A) parameter in our model. Within this area, the camera trap grid installed detected six other *P. maximus* that potentially were transient individuals (Supplementary Data SD3). Based on our monitoring of the area, we assumed there could be between 10 and 13 resident individuals in the area (N). We sorted values of home-range area (H) from the estimated maximum likelihood AKDE, and values of overlap (O) from the observed overlap values and estimated a median density of 7.65 individuals per 100 km² ($CI = 5.68$ – 10.19 ind/100 km²). We also performed the same procedure accounting for the transient individuals, assuming that there could be between 10 and 18 individuals in the area, and estimated a median density of 7.68 individuals per 100 km² ($CI = 5.7$ – 10.27 ind/100 km²).

DISCUSSION

Capture and monitoring.—There has been an increase in field studies of *P. maximus* in recent years (e.g., Aya-Cuero et al. 2017; Quiroga et al. 2017), nevertheless, capture and tracking in the wild has rarely been attempted. Furthermore, previous studies only have been able to capture a limited number of individuals (e.g., $n = 2$ —Carter and Encarnação 1983; $n = 1$ —Leite-Pitman et al. 2004; $n = 9$ —Silveira et al. 2009), with only short monitoring periods through VHF telemetry (e.g., mean = 27 days—Silveira et al. 2009). To our knowledge, the present study is the longest and most comprehensive undertaken on spatial ecology of giant armadillo to date, and the first to apply GPS monitoring telemetry techniques.

Both intra-abdominal VHF transmitters and externally attached GPS devices proved to be safe (causing no injuries or casualties) and efficient techniques to monitor *P. maximus*. Intra-abdominal transmitters allowed the monitoring of individuals over multiple years. However, due to the large home-range areas of the species, and the limitations of the intra-abdominal transmitter's signal range, we were unable to find the animals in the course of every monitoring attempt; a large number of days in the field was required to keep track of tagged individuals. On the other hand, even though GPS devices fell off the animals after relatively short periods (1 to 3 months), this method generated large amounts of data with high temporal resolution and required comparatively less human effort postcapture.

Home range and daily displacement.—Estimated home range for *P. maximus* at our study site was larger than previously reported (300–1,500 ha—Carter and Encarnação 1983; Noss et al. 2004; Silveira et al. 2009). Differences between our estimates and those of other studies could be due to our larger data set of locations per individual or our longer average

monitoring period. [Silveira et al. \(2009\)](#), who had the largest data set to date, monitored five animals for an average of 27 days and gathered 115 locations, whereas we had an average monitoring period of 69 days and a median of 548 locations per individual.

Median adult daily displacement at our study site is smaller than that reported by [Noss et al. \(2004\)](#) in Bolivia (3.7 km), larger than that found by [Encarnaç o \(1986\)](#) in Southeastern Brazil (0.3 km) and similar to the average distance reported by [Silveira et al. \(2009\)](#); 1.8 ± 1.4 km) in Central Brazil. In addition, the maximum distance reported here (2.57 km) is similar to the 2.7 km reported by [Carter \(1985\)](#) in Brazil. However, these studies used different methods for individual monitoring and displacement estimation: comparisons should, therefore, be made with caution. Here, we used GPS telemetry data with a high temporal and spatial resolution, providing a high confidence level for this type of estimate.

Space use.—The effect of body mass on home range is given through its influence over daily displacement. Home-range size and daily displacement are primarily related to the energetic requirements of a species but are also influenced by intra- and interspecific interactions, habitat productivity, and resource patchiness ([Harestad and Bunnell 1979](#); [Sandell 1989](#)). *Priodontes maximus* are insectivorous specialists, with a low-calorie myrmecophagous diet ([Redford 1985](#); [Anacleto and Marinho-Filho 2001](#); [Anacleto 2007](#)). As social insects are encountered concentrated in small patches scattered unpredictably throughout the landscape, *P. maximus* must establish large home ranges, and frequently change shelters to meet their energetic requirements, corroborating the predictions of [McDonough and Loughry \(2008\)](#). Larger individuals need to range over a greater area to meet their daily energetic requirements ([Harestad and Bunnell 1979](#); [Jetz et al. 2004](#)). Since males and females of similar body mass tend to travel similar distances daily, patterns of daily displacement seem to be mostly related to the species' energetic requirements.

Although daily displacement distances may be similar, males and females seem to adopt different space use strategies regarding home-range size. Females occupy smaller areas, which end up being intensively used, whereas males range over a larger area with comparatively lower density of use, indicating that energetic requirements are not the only factor influencing the species space use strategy. Male space use and space sharing patterns can be related to the distribution of receptive females ([Clutton-Brock et al. 1989](#)). When females of a population are encountered at low densities, male territories tend to cover large extents with low density of use, since they have to range over large areas to increase the chances of encountering receptive females ([Clutton-Brock et al. 1989](#)). This seems to be the case, since *P. maximus* occur at naturally low densities ([Carter et al. 2016](#)) and females in our study area maintained almost exclusive home ranges. Even though little is known about the mating behavior of *P. maximus*, the observed patterns of space use and overlap, where females present smaller, nonoverlapping home ranges and males present larger ranges overlapping with both males and females, suggests a promiscuous or polygynous

social mating system ([Clutton-Brock et al. 1989](#)). In these types of mating system, males may mate with more than one receptive female ([Clutton-Brock et al. 1989](#)). Further studies, such as genetic paternity and maternity analyses, could help us confirm and better understand the mating system and species' biology.

Social interaction.—The likelihood of social interactions can be inferred from the amount of overlap between individuals' home ranges ([Shier and Randall 2004](#)). Our results show that the small areas shared among individuals were used at lower density, reducing static interaction and encounter probability, as previously suggested by [Silveira et al. \(2009\)](#). This corroborates the general pattern that adult *P. maximus* tend to be solitary during most of their lives. Social interactions in this species are known to take place only during breeding activities and while females rear their young ([Carter et al. 2016](#)).

Previous research on armadillos indicates a high likelihood of social interactions being influenced by olfactory cues. Armadillos have anal glands that likely are used for marking burrows, tracks, and other spatial cues. Armadillo secretion is likely to be composed of pheromones used to signal their presence and, likely, their reproductive status ([Dickman 2001](#); [Medri et al. 2011](#)). We observed animals defecating and urinating while digging burrows, effectively leaving olfactory cues. Our camera trap records have shown individuals visiting other individuals' territories, inspecting burrow entrances and their sand mounds, but never effectively occupying burrows dug by other individuals. This observation corroborates the observed overlap pattern, which indicates that animals may use the same areas, but not at high densities. Our observations indicate that these olfactory cues on the sand mounds of burrows are one of the communication strategies of this solitary species.

Despite pairs of individuals presenting a low overall overlap, pairs of males and pairs of males and females presented a higher overlap when compared to pairs of females. This pattern could be the result of male ranging behavior, which generates more areas of less density of use within their territories when compared to females and consequently, larger overlap with other individuals. In addition, males also displayed an exploratory ranging behavior. Camera traps have shown two of our known adult males visiting areas 15 and 20 km away from their home ranges, which could be related to exploratory incursions and/or to searches for receptive females. [Noss et al. \(2004\)](#) suggested a considerable home-range overlap between few males (2–3), and pairs of males and females in Bolivia. Although it has been described that pairs of males and females often overlap ([Noss et al. 2004](#); [Carter et al. 2016](#)), our telemetry data shows that the actual overlap between adults is low and occurs mainly in areas used at low densities. This perceived overlap in camera traps could in fact be due to male short-term exploratory behaviors.

Site fidelity.—Individuals of both sexes showed movement patterns indicative of site fidelity ([Fleming et al. 2014](#); [Calabrese et al. 2016](#)). The continuous use of a determined area, i.e., establishment of a home range and site fidelity, can increase fitness through recognition and reutilization of mapped resources within that area ([B rger et al. 2008](#); [Merkle et al. 2014](#); [Oliveira-Santos et al. 2016](#)). Site fidelity can be advantageous

for a large-sized myrmecophagous species such as *P. maximus* that feeds on sessile insect colonies. Smith (2007) stated that *P. maximus* often destroy the termite nests they feed on and that this behavior would require an almost nomadic behavior rather than establishing a home range. However, our results indicated that *P. maximus* do not adopt a nomadic existence and we have seldom recorded *P. maximus* destroying termite colonies to a point where the colony was not able to reassemble itself. At our study area, termite colonies were recovered after an average period of 1–4 weeks. *Priodontes maximus* ranging behavior within the home range could allow ant and termite colonies to recover before new feeding events. Furthermore, although males and females presented different strategies of ranging behavior within home ranges, we did not find differences in site fidelity between sexes.

The studied individuals occupied the same range over several years. Long-term site fidelity has been recorded for other armadillo species such as the nine-banded armadillo (*Dasybus novemcinctus*). Loughry and McDonough (1998) captured marked individuals of this species in same area across multiple years. *Priodontes maximus* are estimated to live between 12 and 15 years (Nowak 1999) and have been reported to live up to 16 years in captivity (ZIMS 2017). The ability to encounter marked individuals in the same area across multiple years might help us to estimate the species' longevity in the wild. For example, adult female TC4 was already an adult when we first captured her and remains sexually active after 7 years of monitoring. Hence, long-term monitoring can also allow the study of the species' reproductive behavior and, potentially, patterns of juvenile dispersal, which are still unknown.

Minimum population density.—Given its large home-range size and low degree of overlap between individuals, a limited number of *P. maximus* can be sustained in an area, even in well-preserved habitats such as the Pantanal. *Priodontes maximus* is considered a naturally rare species throughout its distribution (Meritt 2006; Carter et al. 2016) and the density estimates for this species in the Pantanal are similar to those reported for large carnivores such as the jaguar (*Panthera onca*—Soisalo and Cavalcanti 2006). The minimum density estimated for our Pantanal study site (7.65 ind/100 km²) is higher than estimates made from camera trap sampling obtained at other sites in Brazil (1.27–5.55 ind/100 km²—Carter 1983; Silveira et al. 2009) and throughout South America (5.77–6.28 ind/100 km²—Noss et al. 2004; Aya-Cuero et al. 2017). The higher population density reported in this study could be related to habitat integrity of the Pantanal (Harris et al. 2005). However, the higher density estimates also could be related to the method and long duration of the study. Furthermore, previous studies using camera traps were actually set up to study multiple species or large felines, and had a low recapture rate (e.g., Noss et al. 2004; Silveira et al. 2009).

This study contributes to the ecology and natural history knowledge framework of *P. maximus*. We were able to characterize *P. maximus* as a generally asocial species, most likely promiscuous/polygynous, that establishes large and long-term

home ranges, which grants the population a naturally low density. The intensive GPS monitoring methods allowed us to estimate measures of daily displacement with unprecedented accuracy; the long-term monitoring period (multiple years) provided a high confidence to home-range area estimates. Clear measures of home-range size can aid in defining the spatial scale of effective management efforts for species conservation (Stewart et al. 2016). In situ conservation is especially important for *P. maximus*, because the species does not reproduce in captivity, and reintroduction is, therefore, not a viable conservation measure (Carter et al. 2016). Spatial patterns and biological characteristics such as the ones obtained in this study should be used to guide future conservation strategies for the giant armadillo.

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Parameters for the Continuous Time Movement Model with the best fit to describe each individual's movement behavior.

Supplementary Data SD2.—Complete script for the R code developed for the canonical density estimation and bootstrapping procedures.

Supplementary Data SD3.—Identification and photographs of the 21 individuals of giant armadillo (*Priodontes maximus*) detected in the study site exclusively by camera traps.

Supplementary Data SD4.—Sampling effort, home-range estimates, daily displacement estimates, movement model, and individual information on the 29 individuals of *Priodontes maximus* captured at Baía das Pedras ranch, Corumbá, Brazil, from October 2011 until January 2018.

Supplementary Data SD5.—Diagram and coefficients of the Structural Equation Model (SEM) built to explain the relationship between home-range area (KDE 95%), daily displacement, sex, and body mass, of individuals.

Supplementary Data SD6.—Coefficients of the Structural Equation Model (SEM) built to evaluate the relationship between home-range area (AKDE 95%), daily displacement, sampling effort, sex, and body mass of individuals.

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