



## Research Article

## Life stage, sex, and behavior shape habitat selection and influence conservation strategies for a threatened fossorial mammal

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## Abstract

Resource selection provides essential information about species strategies to meet their biological requirements, and is key for conservation strategies development. Although intraspecific variation in behavior is widespread, most resource selection studies have ignored intrapopulation variability. We aim to understand if individuals have different habitat selection preferences depending on life stage, sex, and behavioral state. As a model, we use the vulnerable fossorial giant armadillo *Priodontes maximus* in the Pantanal. We tracked 23 individuals between 2010 and 2018 using telemetry (12240 locations). Habitat selection during activity and rest were estimated using step and resource selection functions, respectively. Giant armadillos selected different landscape features according to sex, life stage and behavioral state highlighting the potential bias in habitat selection studies based only on one life stage or behavioral state, especially for fossorial species. Younger individuals presented higher selection strength of forests, with denser vegetation and less predation risk, for activity and rest, which is not common for species with long parental care. Sexual differences evidenced that females, which are exclusively responsible for parental care, presented stronger selection of forests and closed savannas during rest. Closed savannas, with high food availability, were selected for activity irrespective of sex or age. Floodable areas were selected only by adult males, presumably to improve mobility. Our findings indicated that females select habitats in a way to balance offspring safety and food availability, while males are risk takers and explore space widely. Forests showed to be fundamental for the species survival, especially during early life stages. Unfortunately, harmful management practices recently adopted, e.g., conversion of forests into pasture and fires, affect the habitats selected by this ecosystem engineer. Giant armadillos can act as umbrella species, as strategies targeted at protecting this charismatic large mammal could provide wider benefits for biodiversity conservation and ecosystem services in the Pantanal.

## Introduction

Habitat selection results from the balance between gains (e.g. food availability) and costs (e.g. predation risk; Clutton-Brock et al., 1987), serving as proxy for individual fitness (e.g. reproductive success; Uboni et al., 2017). The understanding of habitat requirements of threatened species allows us to estimate the potential impacts of habitat changes due to management practices used by landowners and recommend best practices (Stewart et al., 2019). Nevertheless, if intrapopulation differences in habitat selection are detected (e.g. between age classes, sexes or even behavior), this would need to be taken into account when developing these strategies. Multiple intrinsic (e.g. physiology) and extrinsic factors (e.g. intraspecific relationships) can influence movement and habitat selection patterns of individuals (Bartolino et al., 2011; Nathan et al., 2008). Patterns of resource selection can change along an individual life cycle due to changes in selective pressures for individuals of different sizes and age classes (e.g. predation risk, physiology and resource requirements; Bartolino et al., 2011;

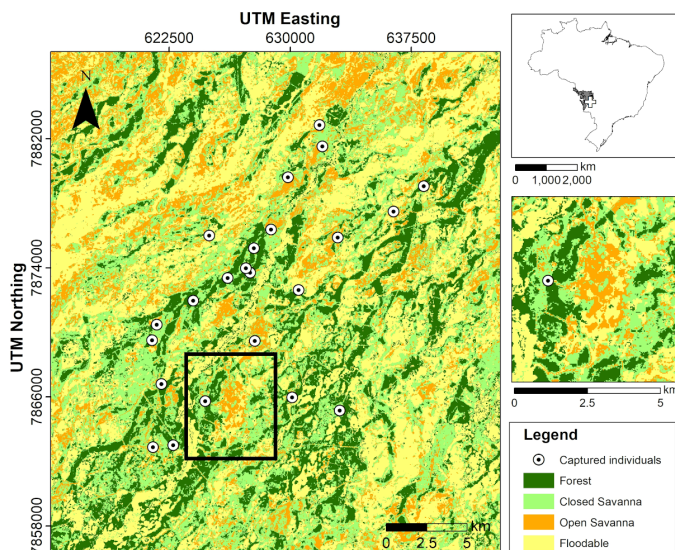
Imansyah et al., 2008; Schupp, 1995). This is relevant for species conservation because if, for example, strategies are based mainly on adult behavior and, juveniles present different habitat and resource requirements, juvenile recruitment could be affected (Paterson et al., 2012; Schupp, 1995).

Depending on the species morphology, biology and mating system, individuals of different sexes might present different behavioral strategies and selection patterns in order to decrease predation susceptibility and increase individual Darwinian fitness (Saïd et al., 2012; Bartelt et al., 2004; Main et al., 1996). According to the predation-risk hypothesis for mammals, females tend to trade off food quality of habitats to favor offspring safety, since female reproductive success is given by offspring survival. On the other hand, males achieve reproductive success by finding mates and tend to select habitats with high-energy gain and potentially higher risk, given that males are not involved in parental care activities and adults are less susceptible to predation (Main et al., 1996; Clutton-Brock et al., 1987).

Behavioral state can also influence resource selection. Selection during rest/sleep periods indicates where animals find suitable habitat to establish shelters and burrows, which are especially important elements

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**Figure 1** – Landscape structure of the region where the twenty-three giant armadillos *Priodontes maximus* (white circles) were captured between July 2010 until January 2018. In the upper right, the location of our study site (cross), in the Pantanal wetlands (grey) of Mato Grosso do Sul state, Midwestern Brazil. In the inset, a close-up on the landscape structure near the capture location of one of the armadillos.

of fossorial and semi-fossorial species ecology. On the other hand, resource selection during activity periods indicate where animals can find suitable conditions for foraging, moving and searching for mating partners (Attias, 2017). Hence, conservation efforts can be hampered if habitat requirements differ between behavioral states (e.g. sheltering and foraging) and this is not taken into account.

The giant armadillo *Priodontes maximus* Kerr, 1792 (Mammalia: Cingulata) is a cryptic fossorial South American species. They occur at low densities and have a low population growth rate, which limits its ability to recover from anthropogenic disturbances (Desbiez et al., 2020a,b). The species is currently classified as “Vulnerable” (A2cd) on the IUCN Red List of Threatened Species due to habitat loss, hunting and illegal animal trafficking (Anacleto et al., 2014). *Priodontes maximus* dig deep excavations to both feed and rest. This behavior influences resource availability for at least 70 other species, granting *P. maximus* the role of an allogenic physical ecosystem engineer (Desbiez and Kluyber, 2013).

Based mainly on the presence of their characteristic excavations and on few individuals captured, *P. maximus* has been reported to occur in humid to dry lowland forests (Carter et al., 2016; Noss et al., 2004; Emmons and Feer, 1997; Cabrera and Yepes, 1940), using open habitats (Silveira et al., 2009), closed savannas (Anacleto, 1997) and forests (Merritt, 2008). However, the occurrence of an animal or its traces in a given type of habitat does not imply that the individual actually selected this habitat feature — i.e. used it disproportionately to its availability (Beyer et al., 2010; Johnson, 1980). These indirect evidences of the species and the few individuals tracked to date have not allowed the study of resource selection for this species, but rather descriptions of where evidence has been found (e.g. Silveira et al., 2009; Anacleto, 1997). Furthermore, due to the nature of the available data, previous studies could not take into consideration intra-population variability or differences between behavioral states, which are especially relevant aspects for this long-lived species, with a long juvenile phase, that spends the day underground sheltering and the night above ground foraging (Desbiez et al., 2019).

The highest densities of the rare *P. maximus* have been recorded on private cattle ranches in the Brazilian Pantanal (Desbiez et al., 2020a). Unfortunately, in the recent past, there has been an increase in the conversion rates of natural landscapes in this region mainly due to the conversion of woodlands into exotic pastures and use of seasonal prescribed fires (Alho, 2008). This is worrisome since habitat conversion, fires and grazing pressure are considered some of the main threats to biodiversity conservation in South America (Jarvis et al., 2010) and

habitat loss and degradation are the primary causes of biodiversity decline worldwide (Haddad et al., 2015).

In this context, we aimed to understand if individuals have different habitat selection preferences depending on life stage, sex, and behavioral state. As a model, we used the vulnerable fossorial *P. maximus* in private cattle ranches of the Brazilian Pantanal. We expected: (1) adults to select safer habitats for resting and habitats with more food resource availability when active; (2) juveniles to select safer habitat features, regardless of activity status or sex, when compared to adults; (3) adult females to select habitats in a way to balance offspring safety and food resource availability; and (4) adult males to use the landscape more widely, selecting habitat types that maximize food resource and mate encounter, as predicted by the predation-risk hypothesis.

## Material and Methods

### Study area

The Pantanal is a 140 000 km<sup>2</sup> floodplain that holds some of the largest known populations of several threatened mammals (Harris et al., 2005). This study was carried out between July 2010 and January 2018, in a 350 km<sup>2</sup> area that includes seven traditionally managed cattle ranches (19°16'60" S, 55°42'60" W) in the Nhecolândia sub-region of the Brazilian Pantanal. Historical mean temperature is 25.4 °C, climate is classified as semi-humid tropical (Aw), with a hot, rainy season (October to March), and warm drier season (April to September; Soriano, 2000).

The landscape of this region is a mosaic of different habitats that include permanent and temporary ponds, natural and exotic open grassland, open savanna, closed savanna and semi-deciduous forest (Abdon et al., 1998; Fig. 1). Our study area lacks watercourses, but presents widespread flooding during the rainy season. Floodable areas are covered by grassland and sparse shrubs during the dry season, and completely or partially flooded during the flood season. Higher areas that are not subjected to flooding are covered by denser vegetation, such as closed savanna and semi-deciduous forests (Harris et al., 2005). Areas of closed savanna include a landscape feature characteristic of the Pantanal and other savannas, the “murundu”. “Murundus” are small round-shaped island-like mounds, composed of soil, clay and/or sand, that can be 0.1 to three meters high, and one to 20 meters wide (Borges and Tomás, 2008). These discrete features are covered by dense Cerrado vegetation and usually present at least one termite nest in its center. Due to its height, they are rarely subject to flooding, but can be surrounded by water during floods. Closed savannas at our study areas are composed of many “murundus” interspersed by grassland.

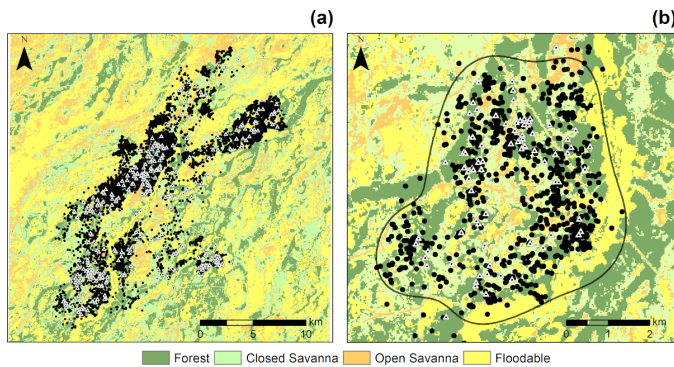
Only 2.5% of the Pantanal’s territory is formally protected and most land is privately owned and used for traditional extensive cattle ranching (Harris et al., 2005). Under this type of management cattle is raised in natural grassland and woodlands are preserved. Hence, anthropogenic threats in the study area are low overall (with limited habitat loss, limited hunting and no paved roads). Unfortunately, due to cultural and economic changes, there has been an increasing conversion rate of the native vegetation in the Pantanal in recent past and areas of woodland (i.e. forest and closed savanna) are being converted, mainly, into grasslands (Miranda et al., 2018).

### Capture, handling and monitoring

We followed the capture and handling procedures described in Desbiez et al. (2020a). Once captured, we chemically immobilized animals to collect individual information and implant intra-abdominal VHF radio transmitters (IMP 310, Telonics, Inc., Mesa, AZ — weight = 38.5 g, i.e. 1.3% of armadillo’s average body mass; Desbiez et al., 2020a; Hernandez et al., 2010; Silveira et al., 2009). Once procedures were terminated, anesthesia was reversed and, after full recovery in a ventilated wooden box, animals were released in the same burrow they were captured (Desbiez et al., 2020a).

Animals were monitored for 15 days per month on average. Monitoring to locate animals resting inside burrows was accomplished through VHF telemetry using the homing-in to the animal technique (Samuel





**Figure 2** – Telemetry locations of the twenty-three giant armadillos (*Priodontes maximus*) tracked at Baía das Pedras ranch, Aquidauana, Brazil, from July 2010 until January 2018. GPS telemetry activity records are represented by black circles and VHF telemetry burrow locations are represented by white triangles. (a) Locations for all armadillos monitored. (b) Example of locations recorded within an individual's home range (female - TC04, monitored between October 2011 until October 2015) to enable detailed visualization of the dataset of habitat use and habitat availability.

and Fuller, 1994). Once encountered, burrow location was recorded using a hand held GPS. In addition, most animals were temporarily fitted with a GPS tracking device (TGW-4100-2, Telonics, Inc., Mesa, AZ — 71 g i.e. 2.37% of armadillo's body mass) at the moment of first capture and/or through recaptures during monitoring. GPS devices were externally attached to the animal's carapace, while anesthetized, following the methods previously used by Silveira et al. (2009). Devices obtained fixes with 30 minutes intervals between 1800 h and 0400 h, when animals were most likely to be active according to preliminary camera trap records. Due to the depth of *P. maximus* burrows, GPS devices only recorded locations when animals were active and above ground. Hence, all GPS records were identified as activity records.

### Data analysis

Using ArcMap 10.5, we combined the bands 4, 3, and 2 (in this order) of Landsat 8 imagery obtained in 2018 to perform a supervised classification of the landscape features at our study site. Habitat type of the study site was characterized according to vegetation cover and summarized in the following categories: forest (18.85% of the study area), closed savanna (27.14%), open savanna (18.6%), and floodable areas (35.36%; Fig. 1).

We characterized habitat selection of *P. maximus* during activity, using GPS locations, and during resting periods, using VHF locations of burrows in use. Due to the high temporal resolution of the GPS data and the regular time interval between fixes we used Step Selection Functions (SSF; Forester et al., 2009; Fortin et al., 2005) to evaluate habitat selection during activity. For each actual location of each armadillo, we generated 30 random possible steps, sorting from the observed distribution step lengths and turning angles. This approach enables accounting for changes in resource availability while animal moves across space. We recorded the habitat type at the end-point of each used and available random step of each armadillo. We fitted the SSF using a Conditional Logistic Regression (CLR) using the function `clogit` in the package `survival` (Therneau, 2015) in R (R Development Core Team, 2019). The CLR model was conditioned to each step within individual (where observed steps were scored as one and random available steps were scored as 0).

Given the variable time lag between VHF locations for the same individual, we used Resource Selection Functions (RSF; Manly et al., 2002) to characterize habitat selection during the resting period, i.e. burrow locations. To maintain a similar spatial scale to that used in the SSF model, we evaluated third-order individual-level selection (*sensu* Meyer and Thuiller, 2006) of burrow locations. Hence, we recorded the habitat type for each of the 1159 VHF burrow locations to characterize habitat use, and for 1159 random locations, to characterize habitat availability. Random locations were sorted from the home range area of the monitored individuals using the function `spsample` in the package `sp` (Pebesma and Bivand, 2005). To characterize home range

area we used Autocorrelated Kernel Density Estimates (AKDE 95%; Fleming et al., 2015), in the same manner as described in Desbiez et al. (2020a), through the package CTMM (Fleming and Calabrese, 2018). The RSF model was fitted using CLR, which was conditioned by individual identity. Observed locations were scored as one and random locations were scored as zero.

Because multiple factors can influence habitat selection, we fitted four different models for each data set (i.e. activity and rest): one accounting only for the effects of habitat type; one accounting for the effects of habitat type and sex of individuals; one accounting for the effects of habitat type and body mass of individuals; and one accounting for the effects of habitat type, sex and body mass of individuals. We used Akaike's Information Criterion (AIC) for model ranking through the function `aictab` of the `AICcmodavg` package (Mazerolle, 2019). Results of the best-ranked model were plotted using the relative selection strength of each habitat type, which was interpreted as the effect size, i.e., the exponential value of the model coefficients (Avgar et al., 2017; Forester et al., 2009). For model interpretation, we used a weight of approximately 30 kg as a threshold between adult and juvenile individuals as suggested by Desbiez et al. (2019) morphometry study.

## Results

In a period of eight years, we captured and monitored 23 *P. maximus* (13 F, 10 M) through telemetry methods (Tab. S1). Fifteen of these individuals were adults, with mean body mass of 33 kg (28.6–36.9), and eight were juveniles, with mean body mass of 25.6 kg (18–30.4). Animals were monitored for a median time span of  $372 \pm 545$  days (min=34, max=1862 days). We gathered 11081 GPS activity records and 1159 VHF records of inactivity (Fig. 2).

Locations of resting sites were found mainly in forests (48.7%), followed by closed savannas (38.6%), floodable areas (8.1%) and open savannas (4.6%). The best-ranked model to explain resource selection during rest took into consideration not only the habitat type but also individual body mass and sex (Tab. 1). For resource selection during activity, the two best-ranked models took into consideration habitat type and sex, and habitat type, sex and body mass (Tab. 2). We plotted the latter model to allow comparisons between the models for the two behavioral states (Fig. 3).

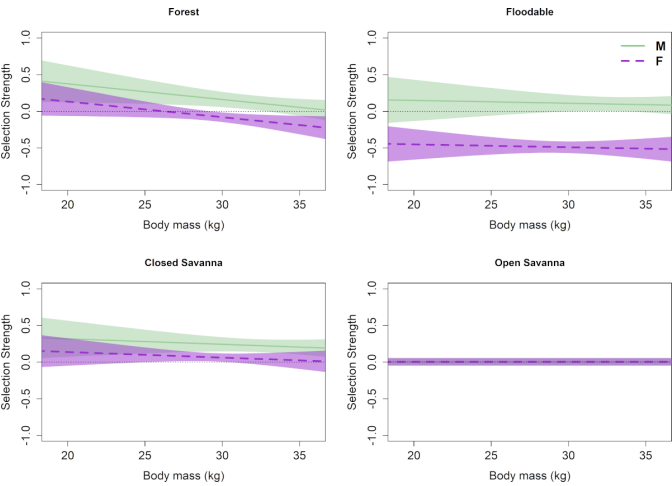
Most activity records were located in closed savannas (39.6%), followed by forests (29.2%), floodable areas (17.4%) and open savannas (13.9%). The selected SSF model showed that, during activity, lighter individuals showed stronger selection of forests than heavier ones and males showed a stronger selection pattern than females (Fig. 3). Floodable areas were selected by males and avoided by females during activity, regardless of body mass. Individuals of both sexes selected closed savannas for activity, regardless of body mass. However, the selection strength of closed savannas was stronger for males. Finally, open savannas were used according to their availability during activity, regardless of sex or body mass.

For burrow locations, the RSF model shows that *P. maximus* selected mainly forests. Nevertheless, selection strength of forests was stronger for females, when compared to males, and for lighter individuals of both sexes (Fig. 4). Floodable areas were avoided for resting by both sexes, especially for heavier individuals. Closed savannas were selected by females and avoided by males, regardless of body mass. Finally, open savannas were avoided for resting, regardless of sex and body mass. See Supplemental materials for coefficients of both SSF (Tab. S2) and RSF models (Tab. S3). Fig. 5 provides a visual summary of the selection patterns encountered during activity and rest for animals according to age class.

## Discussion

### Variation in resource selection patterns

We demonstrated that, as hypothesized, *P. maximus* selects different landscape features according to life stage, behavioral state and sex. The intensive and long-term GPS monitoring techniques applied generated unprecedented fine-scale resource selection information associated to

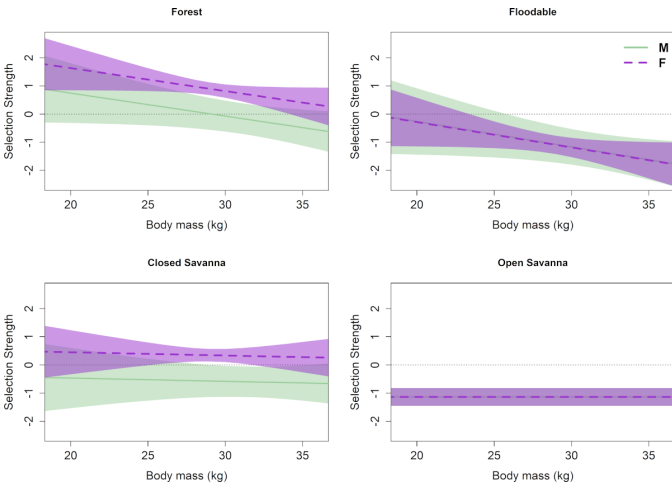


**Figure 3** – Habitat selection of giant armadillo *Priodontes maximus* during activity according to individual body mass and sex. Male relative selection strength is represented by solid lines (mean) with green shading (SD), and female relative selection strength is represented by dashed lines (mean) with purple shading (SD). Individual plots present armadillo selection strength for each habitat type (forest, closed savanna, open savanna and floodable areas): values above 0 indicate selection; values below 0 indicate avoidance; and values close to 0 indicate use according to availability. Data from twenty-three individuals tracked at Baía das Pedras ranch, Aquidauana, Brazil, from July 2010 until January 2018.

behavioral data and individual information. Hence, previous studies with small sample sizes are unlikely to have captured the behavioral patterns and variability expected in a population. Furthermore, this study reveals the potential bias of habitat selection studies of fossorial and semi-fossorial animals that are often based only on burrow locations or detection methods that only record animals during activity (e.g. camera traps).

*Priodontes maximus* selected forests for both activity and rest in the Pantanal. The broad use of humid to dry lowland forests by *P. maximus* has been reported for several localities (Carter et al., 2016; Noss et al., 2004; Emmons and Feer, 1997; Cabrera and Yepes, 1940). Aya-Cuero et al. (2017) recorded *P. maximus* building burrows at riparian forest habitats in Colombia and associated the use of this type of habitat to increased availability of ants and termites. Nevertheless, although ants and termites build their nests in dry patches within forests in the Pantanal (Mathews, 1977), their highest densities are found in other habitat types (Anacleto, 1997).

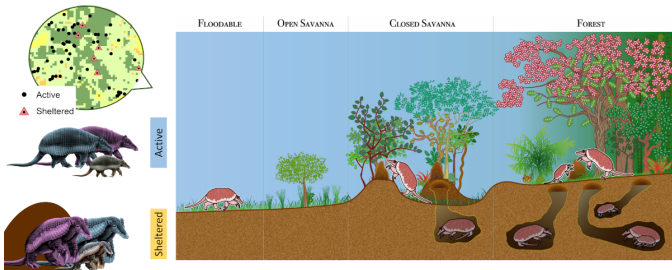
For burrow excavation and resting, *P. maximus* selected mainly higher ground forests and closed savannas (Fig. 5). In contrast with the lower ground vegetation types, these vegetation types are less affected by flooding events, since they are above the underlying water table (Harris et al., 2005), helping to keep the burrows dry. Anacleto (1997) encountered evidences of *P. maximus* burrowing and foraging mainly in closed savannas (“cerrado”), but also in forested areas, open savannas and grasslands. However, the description of burrowing activities in lowland and open vegetation types could be due to potential misidentifications of feeding holes as sleeping burrows. *Priodontes maximus* spends 80% of its time underground inside its burrows, where it rest and shelter from predators and unfavorable environmental con-



**Figure 4** – Habitat selection of giant armadillo *Priodontes maximus* during rest according to individual body mass and sex. Male relative selection strength is represented by solid lines (mean) with green shading (SD), and female relative selection strength is represented by dashed lines (mean) with purple shading (SD). Individual plots present armadillo selection strength for each habitat type (forest, closed savanna, open savanna and floodable areas): values above 0 indicate selection; values below 0 indicate avoidance; and values close to 0 indicate use according to availability. Data from twenty-three individuals tracked at Baía das Pedras ranch, Aquidauana, Brazil, from July 2010 until January 2018.

ditions (Desbiez and Kluyber, 2013; González et al., 2001). Therefore, burrow location selection plays an important role for individual fitness and survival.

Forests were selected by adult females for burrow excavation and by juvenile individuals of both sexes for activity and rest. This tendency could be related to increased predation risk of juveniles, female parental care behavior and/or thermoregulation strategies. Females with offspring tend to choose safer habitat types, even at the expense of resource availability (Saïd et al., 2012; Main et al., 1996; Clutton-Brock et al., 1987). Despite the lower availability of food resources (Anacleto, 1997), forests have denser vegetation and arboreal cover, which potentially decreases armadillo detection and predation risk. Hence, the selection of forests by adults for burrow excavation, especially by adult females, and overall by juveniles corroborates the predation-risk hypothesis and our initial hypotheses. In addition, forests can also buffer air temperature variation, which can be important for basoendotherms such as *P. maximus* and especially advantageous for smaller individuals, with less thermal inertia for thermoregulation and energy conservation (Attias et al., 2018; Maccarini et al., 2015). *Priodontes maximus* burrows inside forests maintain a nearly constant temperature of  $25.5 \pm 1.98^\circ\text{C}$  (Desbiez and Kluyber, 2013).



**Figure 5** – Visual representation of the habitat selection patterns by giant armadillos *Priodontes maximus* in relation to the available vegetation types in the Pantanal wetlands of Mato Grosso do Sul state, Midwestern Brazil. Armadillo size is indicative of armadillo age class; large armadillos portray adults and small armadillos portray juveniles. Armadillos above ground represent selection patterns of individuals during activity and armadillos underground, in burrows, represent selection patterns during rest. Available habitats are classified in four categories: Floodable areas (grasslands and sparse shrubs during the dry season and flooded during the flood season); Open savannas (flooded for relatively shorter periods and covered by sparse vegetation); Closed savannas (round mounds of soil covered by dense Cerrado vegetation – “murundus” – interspersed by grassland); and Forest (semi-deciduous forest vegetation).

**Table 1** – Ranking of the four competing resource selection function models fitted to characterize habitat selection by *Priodontes maximus* during rest. Models account for the effects of vegetation cover type (“Habitat”), individual body mass (“Mass”) and individual sex (“Sex”). Number of parameters (k), relative difference between models ( $\Delta\text{AICc}$ ), weight of the model (w), cumulative weight (cum w) and log likelihood (LL). Data from twenty-three individuals tracked at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

| Model            | k  | LL       | $\Delta\text{AICc}$ | w    | cum w |
|------------------|----|----------|---------------------|------|-------|
| Habitat:Sex:Mass | 11 | −1419.60 | 0.00                | 0.90 | 0.90  |
| Habitat:Sex      | 7  | −1426.43 | 5.61                | 0.05 | 0.96  |
| Habitat:Mass     | 7  | −1426.73 | 6.21                | 0.04 | 1.00  |
| Habitat          | 3  | −1440.91 | 26.51               | 0.00 | 1.00  |

The most dynamic changes within an individual's life history often occur in the early life phases, often reflecting greater selection pressures on survival (Imansyah et al., 2008). Differences in the spatial ecology suggest that different selection pressures may affect *P. maximus* of different age classes (Paterson et al., 2012). Although ontogenetic differences in habitat selection are usually observed for species without parental care behavior, such as plants, fishes, lizards and turtles (Paterson et al., 2012; Bartolino et al., 2011; Imansyah et al., 2008; Schupp, 1995), *P. maximus* presents a long period of parental care, with females caring for their offspring for over a year after birth. Furthermore, juveniles present slow growth rates and reach sexual maturity only at around seven to eight years of age (Desbiez et al., 2019, 2020b; Luba et al., 2020), being subject to different pressures (e.g. increased predation risk) for a long period of their lives.

Closed savannas were selected by both sexes and age classes for activity and by females for burrow excavation and rest. The selection of closed savannas could be related to increased food resource availability in these areas. Closed savanna areas covered by Cerrado vegetation, such as the “murundus”, have the highest relative abundance of ant and termite nests when compared to the other common habitat features of Brazilian savannas (Anacleto, 1997). Hence, the use of this habitat feature for burrowing by females corroborates hypothesis 3, that females would select habitats in a way to balance offspring safety and food resource availability.

Open savannas and floodable areas were avoided for resting, regardless of sex. These two habitat features present reduced vegetation cover and could leave animals more vulnerable to climatic events, such as temperature extremes and wind as well as make the large burrows more conspicuous, making animals vulnerable to predators. Nevertheless, during activity, floodable areas were selected by males, but avoided by females.

Differences in resource selection patterns between sexes can be related to differences in their movement and reproductive behaviors. Male *P. maximus* range over large areas, presenting an exploratory movement behavior that is not exclusively governed by its energetic requirements. Meanwhile, females select primarily areas of denser vegetation and do not overlap their relatively small home ranges with those of other females (Desbiez et al., 2020a). The Pantanal landscape is a natural mosaic composed of areas of denser vegetation interspersed by floodable areas. Hence, even though floodable areas are relatively poor in food resources, they may have been selected by males to improve their mobility between multiple areas of exclusive use by females, potentially increasing their chances of mate encounter. This pattern, associated with the previously described pattern of forest and closed savanna selection, corroborates hypothesis 4, that adult males are risk takers and explore space more widely, selecting habitat types that maximize not only food resource but also mate encounter.

## Coupling land management and species conservation

Adult *P. maximus* require, on average, 25 km<sup>2</sup> with almost exclusive use (Desbiez et al., 2020a). Therefore, large expanses of habitat are required to hold healthy populations of this threatened territorial species and, except in the Amazon, few protected areas within the species Neotropical range possess such an extent to maintain long-term viable

populations. Medium to large sized threatened species with large area requirements need conservation plans that go beyond the establishment of protected areas (Tyrrell et al., 2020). Hence, the development of proper management strategies for landscape features of interest outside protected areas' boundaries is key to these species' conservation. More than half of the native vegetation remaining in Brazil is found in private areas (Sparovek et al., 2012) making them an essential component for biodiversity conservation (Michalski et al., 2010). Therefore, it is important to understand which land use practices on private lands contribute to the maintenance of healthy animal populations (González-Roglich et al., 2012).

Forests are fundamental to the survival of *P. maximus*, especially in their early life stages. This is relevant because captive breeding and reintroduction are currently not viable conservation strategies for this threatened species (Carter et al., 2016). Hence, *in situ* conservation strategies such as targeted habitat protection that can aid, for example, in juvenile survival, could significantly contribute to the conservation of this species that presents a naturally low population growth rate (Desbiez et al., 2019; Carter et al., 2016). Forests also have the highest densities of mammals and are considered the most important habitat feature in the Pantanal in terms of relative energy consumption (Desbiez et al., 2010). The Pantanal is dominated by extensive private lands that have been dedicated to traditional cattle ranching for over 250 years (Harris et al., 2005). This type of activity has proven to be a sustainable management approach that maintains ecosystem function, biodiversity and dynamics of the natural landscape mosaic (Hoogesteijn and Hoogesteijn, 2010; Desbiez et al., 2009; Harris et al., 2005). However, more recently, higher ground forests have been targeted for conversion due to shifts in land management strategies in the Pantanal and about 43% of the area covered by forests has been converted into pasture in the past 15 years (Miranda et al., 2018). Furthermore, it is estimated that, if conversion rates continue to follow the current trend, a complete loss of native vegetation in the Pantanal floodplain can be expected by 2045 (Silva et al., 2011; Alho, 2008). This could strongly affect *P. maximus* recruitment, leading to population declines, and even local extinction. Given its restricted occurrence and key function in the Pantanal landscape, Wantzen et al. (2008) suggest that forests should be fully protected, regardless of the strategy adopted to manage a property.

Closed savanna “murundus” present important food resources for *P. maximus* and their conservation are key to the species' survival. Furthermore, this habitat feature harbors a unique community of both fauna and flora but has received almost no conservation attention (Marimon et al., 2015). Due to its relatively sparse vegetation, the closed savanna areas of “murundus” are particularly targeted for clearing and conversion. When ranchers want to increase the carrying capacity of the land, these areas are converted into exotic pasture, providing the cattle more forage. In addition, fire is another traditional land management technique widely used in the Pantanal that can alter the landscape (Alho, 2008). Fire is used to promote re-growth of pasture, control invasive species, reduce ticks, as well as to burn the vegetation cleared from the “murundus” or forests. Fire usually does not go through the more humid forested areas but spreads through open areas and dry “murundus”. In addition, the biomass accumulated in the “murundus” makes it burn for longer, increasing the risk of injuries for *P. maximus*, especially when resting inside burrows. Even though fire is part of the ecological dynamics of savannas, depending on its intensity, it can kill *P. maximus*. Monitored animals have been found with severe burns, occasionally leading to casualties (suspected three individuals, out of 33 monitored in this study) due to both unintentional and prescribed fires (Silveira et al., 2009; Smith, 2007). After fires, *P. maximus* can continue to use the area (Carter et al., 2016; Prada and Marinho-Filho, 2004), but we have recorded some animals with low body scores (reduced weight and burning injuries) at these sites. However, we propose that, if adhering to specific traditional practices, such as only prescribing fire after the first rains, regular fires can help reduce fuel accumulation, potentially reducing blaze intensity at each fire event, thus reducing mortality risk for *P. maximus* (Carter et al., 2016; Smith, 2007).

**Table 2** – Ranking of the four competing step selection function models fitted to characterize habitat selection by *Priodontes maximus* during its activity. Models account for the effects of vegetation cover type (“Habitat”), individual body mass (“Mass”) and individual sex (“Sex”). Number of parameters (k), relative difference between models ( $\Delta AICc$ ), weight of the model (w), cumulative weight (cum w) and log likelihood (LL). Data from twenty-three individuals tracked at Baía das Pedras ranch, Aquidauana, Brazil, from October 2011 until January 2018.

| Model            | k  | LL         | $\Delta AICc$ | w    | cum w |
|------------------|----|------------|---------------|------|-------|
| Habitat:Sex      | 7  | −37 918.16 | 0.00          | 0.56 | 0.56  |
| Habitat:Sex:Mass | 11 | −37 914.40 | 0.49          | 0.44 | 1.00  |
| Habitat:Mass     | 7  | −37 943.08 | 49.84         | 0.00 | 1.00  |
| Habitat          | 3  | −37 954.21 | 64.10         | 0.00 | 1.99  |

## Conclusion

The maintenance of forested and closed savanna landscapes are essential to the conservation of *P. maximus* in the Pantanal and play an important role for the species reproduction and persistence in this and potentially other eco-regions throughout its distribution. Nevertheless, habitat suitability is species specific and in order to promote the conservation of wildlife communities on private lands it is important to maintain landscape heterogeneity and representation of all habitat types (Silva and Ranieri, 2014) avoiding targeting specific landscape features for anthropic conversion. This is especially important for the conservation of medium and large sized mammal species with large spatial requirements. The key to conserving biodiversity in the Pantanal is preserving the natural habitat matrix that sustains the diversity of landscapes, and to continue integrating cattle into the natural processes that sustain a functioning ecosystem (Desbiez et al., 2009). *Priodontes maximus* possess large area requirement and act as an ecosystem engineer, creating resources used by almost all vertebrate species in the Pantanal (Desbiez and Kluwyer, 2013). Conservation strategies targeted at *P. maximus* protection could provide wider benefits for the biodiversity and ecosystem services in the region. Hence, this charismatic large mammal can play a key role in the conservation of the biological community and can act as an umbrella or flagship species for biodiversity conservation in the Pantanal. 🌿

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Table S1** Information on 23 individuals of *Priodontes maximus* monitored at Baía das Pedras ranch, Corumbá, Brazil, from October 2011 until January 2018.

**Table S2** Model coefficients for the best-ranked resource selection function (RSF) model fitted to characterize resource selection by the giant armadillos *Priodontes maximus* during rest.

**Table S3** Model coefficients for the best-ranked step selection function (SSF) model fitted to characterize resource selection by the giant armadillos *Priodontes maximus* during activity.