



## Habitat selection and home-range use by resident and reintroduced giant anteaters in 2 South American wetlands

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One of the benefits of modeling habitat selection for a given population is the ability to predict patterns in another population that inhabits an ecologically similar area. We studied habitat selection and home ranges of reintroduced and wild giant anteaters (*Myrmecophaga tridactyla*) in 2 South American wetlands (Iberá, Argentina, and Pantanal, Brazil). Nine reintroduced (Iberá) and 10 wild (Pantanal) adult animals were tracked via VHF and GPS between 2007 and 2015. We used resource selection functions to assess habitat selection for the wild anteaters from Pantanal. Generalized linear mixed models were constructed for resting and activity periods during both the wet and dry seasons. We then validated previous models built for reintroduced anteaters in Iberá using data from the wild animals from Pantanal. Habitat type (floodplain, grassland, open savanna, closed savanna, and forest) and distances to selected landscape traits were used as covariates. Locations near forests were positively selected in both populations. Selection of forests in Pantanal was less evident than in Iberá, probably due to the much higher availability of forests in the Brazilian site, with 38–53% of the landscape classified as good-to-high likelihood in Pantanal compared to only 4% in Iberá. Mean home-range size of males was larger in Iberá ( $32.50 \pm 7.64 \text{ km}^2$ ) than in Pantanal ( $14.07 \pm 1.97 \text{ km}^2$ ), whereas home-range sizes of females were similar in both areas ( $9.75 \pm 1.74 \text{ km}^2$  in Iberá;  $9.62 \pm 2.00 \text{ km}^2$  in Pantanal). Results of this study suggest that model validation with geographically independent data is a useful tool to compare reintroduced and wild populations and to identify resources or landscape attributes that are important for a given species, even when these resources are abundant or highly available.

Una de las posibles ventajas de modelar la selección de hábitat de una población es la posibilidad de predecir patrones en otra población que habita un área ecológicamente similar. Se estudió la selección de hábitat y las áreas de acción de osos hormigueros (*Myrmecophaga tridactyla*) reintroducidos y silvestres en dos humedales sudamericanos (Iberá, Argentina, y Pantanal, Brasil). Se monitorearon 9 osos hormigueros adultos reintroducidos (Iberá) y 10 silvestres (Pantanal) a través de VHF y GPS entre 2007 y 2015. Se utilizaron funciones de selección de recursos para evaluar la selección de hábitat de los animales silvestres del Pantanal. Modelos lineales generalizados mixtos fueron construidos para los períodos de descanso y actividad y para las estaciones húmeda y seca. Los modelos previamente construidos para los animales reintroducidos en Iberá, fueron validados con los datos de los animales no translocados del Pantanal. Se utilizaron el tipo de hábitat (planicie de inundación, pastizal, sabana, bosque abierto y bosque continuo) y las distancias a características del paisaje seleccionadas

como variables explicativas. Los sitios cercanos a bosques fueron seleccionados positivamente en ambas poblaciones. La selección de bosques por los animales del Pantanal fue menos evidente que la de los animales de Iberá, probablemente debido a la mayor disponibilidad de bosques en el primer sitio, con un 38–53% del paisaje clasificado como de buena–alta probabilidad de ocurrencia en el Pantanal, comparado con sólo el 4% en Iberá. El tamaño promedio de las áreas de acción de los machos fue mayor en Iberá ( $32.50 \pm 7.64 \text{ km}^2$ ) que en el Pantanal ( $14.07 \pm 1.97 \text{ km}^2$ ), mientras que los tamaños de las áreas de acción en las hembras fueron similares ( $9.75 \pm 1.74 \text{ km}^2$  en Iberá;  $9.62 \pm 2.00 \text{ km}^2$  en Pantanal). Los resultados de este estudio sugieren que la validación de modelos con datos geográficamente independientes es una herramienta útil para comparar poblaciones reintroducidas y silvestres y para identificar recursos o atributos del paisaje que son importantes para una especie, independientemente de su abundancia o disponibilidad.

Key words: forest, habitat use, model validation, *Myrmecophaga tridactyla*, resource availability, resource selection functions

Resource selection functions (RSFs) are frequently used to estimate and predict spatial distributions and resource use by animals (Johnson et al. 2000; Hebblewhite et al. 2005). These models are generally developed using data from a set of used points and a set of available points to identify environmental variables that best predict resource selection by animals (Manly et al. 2002). One of the main benefits of modeling resource selection for a given population is the ability to predict resource selection in another geographic area that is ecologically similar to the area used to create the model (Howlin et al. 2004). Validating RSFs in spatially independent areas can highlight how well these models can be generalized across space and time for a given species and increase the utility of the RSF to wildlife and land managers (Wiens et al. 2008; Coe et al. 2011). For example, RSFs can be used to identify habitats that are important for a species and to assess if reintroduced populations present similar patterns as those of wild populations.

The giant anteater (*Myrmecophaga tridactyla*) occupies a diverse array of tropical and subtropical biomes across its wide range, including grasslands, savannas, and forests (Gardner 2007). Despite this plasticity, giant anteaters seem to prefer environments presenting a mosaic of habitat types, because they generally use forest patches for shelter and rest, and grasslands or shrub savannas for foraging (Shaw et al. 1987; Mourão and Medri 2007; Desbiez and Medri 2010). They appear to tolerate a certain degree of disturbance such as livestock and moderate fires (Shaw et al. 1987; Quiroga et al. 2016). However, they avoid areas with high levels of contact with humans, cattle, and other domestic animals, and they seem to require well-conserved forest patches (Shaw et al. 1987; Di Blanco et al. 2015). Forests are probably an important resource for the species, acting as shelter against extreme temperatures and predation (Camilo-Alves and Mourão 2006; Mourão and Medri 2007). The presence of forests seemed to be essential to the successful reintroduction of this species at the Iberá Marshland region in northeastern Argentina (Di Blanco et al. 2015).

The Iberá Marshland has a physiognomy very similar to the Pantanal (Neiff 2003). The Iberá and Pantanal regions are both freshwater wetland ecosystems where the confluence of different ecoregions forms an intricate complex of marshes, swamps, and shallow lakes and a vast mosaic of sandy plains with flooded grassland, savannas, and forests of different extent. The diversity of habitat types, spatial heterogeneity, and landscape

structure of both regions lead to environments that satisfy the ecological requirements of giant anteaters. By comparing resource selection models between resident and reintroduced animals, we tested if giant anteaters in Iberá were acting as wild giant anteaters would. Patterns of habitat selection that can be generalizable for the species can be used to develop or prioritize conservation and management strategies for giant anteaters and their habitat. They also could be used to evaluate the suitability of other areas for the potential reintroduction of giant anteaters.

Home range is another important spatial characteristic commonly used to describe mammal populations. Home range is defined as the extent of an area with a defined probability of occurrence of an animal during a specified time period (Millsbaugh and Marzluff 2001). Home-range size, location, and shape may change depending on the state of the individual and the conditions of the external environment. Large variation exists in these characteristics within and among different mammal populations (Kie et al. 2002), and studies have been focused on habitat use and selection, and on the spatiotemporal distribution of resources to explain this variability (Robinson 1986; Relyea et al. 2000; Di Bitetti 2001). Home-range size is inversely proportional to resource availability because the area occupied by an animal should be large enough to satisfy its requirements (Schoener 1974). In line with this, differences in home-range sizes between Pantanal and Iberá may be expected according to the relative availability of food resources and refuge at each study site.

The objective of this study was to assess and compare habitat selection and home-range size in 2 independent populations of giant anteaters in similar wetlands of South America, the Iberá Marshland of Argentina and the Pantanal of Brazil. Our 1st hypothesis is that reintroduced giant anteaters will present similar patterns of habitat use as wild animals, with a strong preference for forests, particularly during resting periods. However, we expect less strong selection of forests in the Pantanal region due to the higher availability of this habitat type in relation to Iberá. Our 2nd hypothesis predicts that home ranges will differ significantly between Pantanal and Iberá. We expect larger home ranges in Iberá due to 3 main reasons: 1) the lower availability of forests, which can lead to a higher level of movement to reach this preferred habitat; 2) the higher latitude in Iberá and consequent higher thermal seasonality, which can be

associated with less, or more seasonal, resources; and 3) the reintroduced population might not be in its carrying capacity yet, which may result in animals being able to expand their movements without social constraints in comparison with an established population.

## MATERIALS AND METHODS

*Study site.*—The study took place in 2 different wetlands of South America: the Brazilian Pantanal and the Iberá Marshland region of northeastern Argentina. The Pantanal is one of the world's largest and continuous floodable ecosystems and is located in the center of South America. It is a freshwater floodplain of approximately 160,000 km<sup>2</sup>, of which 80–85% is located in Brazil (approximately 140,000 km<sup>2</sup>). Open grasslands, thick scrublands, savannas, and forests form a mosaic of different landscapes, where vegetation from Amazonia, Cerrado, Atlantic Forest, and Chaco ecoregions coexist (Pott et al. 2011). The Pantanal has a tropical, semi-humid climate and is subject to a predictable annual monomodal flood pulse (Gonçalves et al. 2011). Rainfall varies annually from 800 to 1,600 mm across the region and there is a marked rainy season spanning between November and March (ANA 2005). Seasonal floods last 4–8 months annually, usually between December and May. Thermal seasonality is also present, with mean temperatures ranging from 32°C ± 3°C in the summer to 21°C ± 6°C in the winter, with the lower temperatures occurring between June and August. Nearly 98% of the Pantanal is privately owned (Gottgens et al. 1998), where the main economic activity is extensive cattle ranching for beef, mostly on native pastures (Santos et al. 2002). The study area is located within the Nhecolândia subregion, characterized by the lack of permanent watercourses, and flooding being rain-fed. Cerrado is the dominant vegetation type, with grasslands in lower areas and forest in higher terrain (Silva and Abdon 1998).

The Pantanal study site is centered in the private ranch or “fazenda” Baía das Pedras (17 km<sup>2</sup>, 19°15'S, 55°47'W), where cattle ranching is extensive. This property also receives small groups of eco-tourists for wildlife watching. There are no roads in the area, hunting is uncommon, and overall anthropogenic impact on the landscape is considered low (Desbiez et al. 2010).

The Iberá Marshland region of northeastern Argentina is located approximately 1,000 km south of the Pantanal study site. This region also comprises a diverse mosaic of habitats that result from the confluence of the Atlantic Forest, the Espinal, the Campos y Malezales (Flooded Grasslands and Savannas), and the Chaco ecoregions. A depression, resulting from an ancient course of the Paraná River in the central area of the region, forms a permanently flooded surface of wetlands interconnecting extensive and shallow lagoons united by watercourses of different order. This area is surrounded by higher lands dominated by dry and temporarily flooded grasslands, savannas, and forests (Neiff and Poi de Neiff 2006). Flood level in Iberá depends on rains, which have no clear seasonality. The climate is subtropical, with mean daily temperatures ranging from 16–17°C during the coldest winter months (June–July)

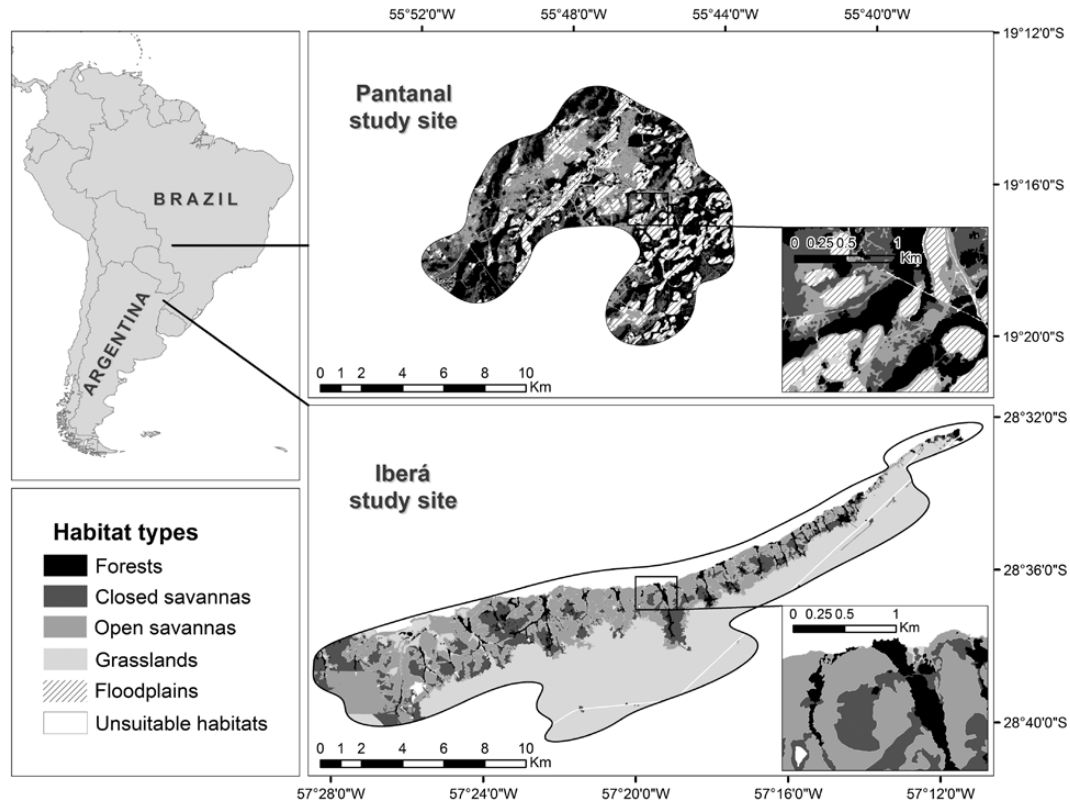
to 27–28°C during the hottest summer months (January–February—Neiff and Poi de Neiff 2006). The Iberá Marshland is protected as a provincial Nature Reserve (approximately 13,000 km<sup>2</sup>) since 1982. The Iberá Nature Reserve (INR) covers the entire upper basin of the Corriente River, the only outflow from the region. About 60% of the INR comprises private properties, 90% of which are located on the land surrounding the permanently flooded habitats. The most common land use in these properties is extensive cattle and sheep ranching, and the second is pine (*Pinus* sp.) plantations.

The 1st reintroduced population of giant anteaters was established in Rincón del Socorro Private Reserve (12.4 km<sup>2</sup>, 28°32'S, 57°10'W), located on the southeastern margin of the INR (Fig. 1), where this study was conducted. This site was a cattle ranch until 2002, when The Conservation Land Trust (CLT) excluded all livestock and started ecological restoration and eco-tourist activities.

Pantanal and Iberá mainly differ in their flooding dynamics. In Iberá, most floodable areas are permanent and concentrated in the center of the region, whereas in the Nhecolândia subregion of the Pantanal flooding is seasonal and more evenly distributed across the landscape. The vegetation units in the Pantanal are correlated with microtopography and seasonal fluctuations in water levels. Even though vegetation composition and species may differ between sites, both areas share a continuous structural gradient of forests to open grasslands which is clearly distinguishable (see Supplementary Data SD1), even though configuration and dominance among habitats differ (see Fig. 1; Table 1).

In both sites we classified the main highland terrestrial habitats into 4 types according to similarities in vegetation structure and contrasts (see Di Blanco et al. 2015 and Supplementary Data SD1 for further description): 1) Forests are characterized by a stratified and complex structure and a continuous canopy cover. Forests are more dominant in the Pantanal study site, covering nearly 40% of the study area, whereas in Iberá they occupy less than 5% of the total area (Fig. 1; Table 1). 2) Closed savannas or scrub forests include small forest patches (< 200 m<sup>2</sup>) and bushes embedded in an herbaceous layer. 3) Open savannas (or open scrub grasslands) are wooded habitats with trees or palm trees very sparsely distributed in space over a short to medium-height herbaceous layer. 4) Grasslands are seasonally flooded habitats dominated by 1.5–2 m high *Andropogon* sp. This type of habitat generally occupies large and continuous surfaces in Iberá, whereas in Pantanal it occupies small and sparse patches surrounding floodplains (see Supplementary Data SD1). These floodplains, locally known as “baías,” are dominated by seasonally flooded grasses that are short in height and structurally similar to open savannas during the dry season. Floodplains occupy important surfaces distributed across the study site in Pantanal (Fig. 1; Table 1). In some of the lower parts of the floodplains in Pantanal, small permanent water ponds are present throughout the dry season.

*Study animals and location data at Pantanal.*—Between July 2013 and October 2015, 10 adult giant anteaters (7 females and 3 males) were fitted and tracked via harnesses equipped



**Fig. 1.**—Study sites and habitat types. The map on the upper left shows the relative location of study sites in South America. The maps on the right show habitat types at each site at 2 different spatial scales: the complete area of analysis based on home ranges of the population studied, and a close-up view (inset) to detail different habitat types. Note the greater relative area covered by forests within the Pantanal site compared to Iberá.

**Table 1.**—Summary of the main habitat types in the study sites (Pantanal in Brazil and Iberá in Argentina), number of locations of giant anteaters (*Myrmecophaga tridactyla*) recorded in each habitat type, and their relative contribution in area and percentage. Habitat classification is based on vegetation structure.

Habitat type	Vegetation structure	Iberá			Pantanal			
		Number of locations	Area (km <sup>2</sup> )	Percentage (%)	Number of locations	Area (km <sup>2</sup> )	Percentage (%)	Percentage including floodplains (%)
Forest	Dense canopy cover, grass understory absent	376	5.59	4.79	495	49.30	50.18	40.85
Closed savanna	Medium canopy cover, bushes and short-medium grass understory	344	19.52	16.72	215	21.25	21.63	17.61
Open savanna	Open canopy cover, short-medium grass understory	141	31.39	26.89	207	26.48	26.95	21.95
Grassland	Tall grass layer of 1.5–2 m height, temporarily flooded	320	60.23	51.70	13	1.22	1.24	1.01
Floodplain	Short grass understory, flooded during wet season				133	22.43		18.58

with GPS and VHF transmitters (MOD 400; Telonics, Mesa, Arizona). Animals were tracked for 50–384 days per individual, mean ( $\pm SE$ ) = 170.5 ( $\pm 37.87$ ) days. GPS locations of individual animals were taken around the clock as frequently as every 20–40 min in order to study other aspects (e.g., movement). This allowed us to estimate if animals were active or

inactive for comparisons with data from Iberá. To account for the error associated with GPS fixes, we considered an animal “inactive” when its location was < 20 m from its preceding location. Inactivity locations were generally grouped for several hours. To make data from Pantanal and Iberá comparable, and to ensure independence of continuous location data,



we randomly selected 1 location per day, and discarded locations within a 24-h period from the preceding location. We demarcated habitat types and associated each location with a specific habitat type (Supplementary Data SD1). We used 1,063 locations of wild animals from Pantanal, with an average ( $\pm SE$ ) of 107 ( $\pm 25$ ) locations per animal.

*Study animals and location data at Iberá.*—Thirty-one giant anteaters were reintroduced at the Iberá study site from October 2007 to December 2013 (Jiménez-Pérez et al. 2016). Released animals had different ages (1–8 years old) and they all came from the Argentinean Chaco region. All animals were fitted with harnesses equipped with VHF transmitters with an activity sensor (MOD 400; Telonics, Mesa, Arizona). For this study, we considered locations gathered from 9 adult reintroduced giant anteaters (5 females and 4 males) that were monitored for a minimum of 6 months. Animals were located by “homing in” and locations were recorded via handheld GPS (see Di Blanco et al. 2015). This allowed us to precisely associate each location with a habitat type, and also to verify if the animal was active (travelling, foraging, other) or inactive (resting or sleeping). We created a map of the different habitats of the study site (Supplementary Data SD1). Locations were sampled around the clock as frequently as once per hour in 24-h periods, and at least once every 30 days. For modeling, we only used the 1st location within a 24-h period, reaching a total of 703 independent locations. Further details are provided in Di Blanco et al. (2015). Management of all giant anteaters has been conducted in accordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016).

*Model building for the Pantanal population.*—We compared locations of anteaters to a set of random “available” locations to determine the maximum-likelihood values of model coefficients (Johnson et al. 2006) in RSFs (Manly et al. 2002). Because of the different numbers of locations per individual (25–248), and for comparison purposes with Iberá animals, we followed individuals to identify a set of used resources, but assessed availability at the population level (Design II approach—Manly et al. 2002). Our analysis corresponded to analyzing resource selection at the spatial scale roughly corresponding to the 3rd order of resource selection as described by Johnson (1980), which represents the selection of habitats or resources within established home ranges. Using the Geospatial Modelling Environment (GME) software (Version 0.7.2.1; Toronto, Ontario, Canada—Beyer 2012), we defined the range estimated for the population, which included all locations for the animals followed in our study. We estimated this area as the 95% isopleth using a fixed Gaussian kernel density estimate function and a bandwidth defined by the least squares cross-validation method (Powell 2000). Availability was defined by drawing 2,000 random locations within the range estimated for the population. We divided these available locations among individuals in the same proportion of used locations to generate a balanced design. For each used and available location, we defined its corresponding habitat type and its distance to forest edge (DFE), distance to human settlements (DHS), and

distance to permanent water ponds (DWP; this last covariate only for dry season) as predictor variables. Distance covariates presented different scales (maximum DFE = 591 m, maximum DHS = 8,940 m); therefore, we rescaled all continuous variables from 0 to 1 for better model performance.

To test for the effects of the explanatory variables on the response variable, we employed generalized linear mixed models (GLMMs—Pinheiro and Bates 2000; Zuur et al. 2009). By including a random effect for individuals, individual variability is identified explicitly and the scope of inference can be extended to the entire population (Neter et al. 1996). Random coefficients force variation in the intercept (Gillies et al. 2006); therefore, we used the individual as random intercept combined with random coefficients of each covariate and combinations to account for the particular weight that any individual may have on the selected fixed component (Supplementary Data SD2). Modeling was performed with a binomial error distribution and a logit link function using the lme4 package (Bates et al. 2011) in R (R Core Team 2016). To select the best structure on both random and fixed components, we followed Zuur et al. (2009). We created a model where the fixed component contained all explanatory variables, known as a “beyond optimal model.” We used this model to find the optimal random structure varying only in its random component. We selected the best random structure using the Akaike Information Criterion (AIC—Burnham and Anderson 2002) estimated through the Laplace method. We also examined the influence of sex, nesting individual with the best combination of covariates in the random component to assess if differences in sex need to be controlled. Once we had the optimal structure of the random component, we searched for the optimal fixed structure of the model to test for the effects of the explanatory variables on the response variable, used versus available locations.

Using the optimal random structure (Supplementary Data SD2), we performed 2 different saturated models (fixed component) for dry and wet seasons (habitat type + DFE + DHS and habitat type + DFE + DHS + DWP, respectively). We used the *dredge* function of the *MuMIn* package (Barton 2016) to obtain AIC scores and relative weights of each competing model. We considered covariates as selected when their 90% CIs did not include zero after averaging all candidate models according to their AIC weight (Barton 2016).

*Validation of Iberá models using geographically independent data.*—Model validation describes the general assessment of the model through the use of data that were not involved in the model-building process. These data can be held out from the original data set or obtained through additional sampling (Howlin et al. 2004).

A simple model developed at Iberá showed a high model fit, explaining an important part of total variation in habitat selection of giant anteaters (Di Blanco et al. 2015). Therefore, we used models developed for reintroduced giant anteaters from Iberá to predict habitat use for resident animals in Pantanal. Habitat type (forest, closed savanna, open savanna, grassland) was defined as a categorical covariate, and DFE and distance to main road (DMR) as continuous covariates for Iberá model

building in RSFs. For model validation, we only included habitat type and DFE as predictors since main roads were not present within the Pantanal study site and DMR was not an important predictor of habitat selection in Iberá (Di Blanco et al. 2015). For Iberá animals, habitat use was modeled by age class (adults, juveniles, and both combined), as well as by activity (active and inactive), and across seasons (Di Blanco et al. 2015). We validated models built for adult animals in Iberá, as all animals captured in the Pantanal study site were adults. Models performed for both active and resting animals at the spatial scale of 3rd-order selection were validated. We defined for each location its corresponding habitat type and its DFE. Floodplains in Pantanal and locations within this habitat type were excluded from the analyses performed for the wet season and were excluded or considered as open savannas only for the dry season analyses. Iberá models were projected in the Pantanal study site, combined and classified into 20 bins based on equal-area percentiles of the predicted relative probabilities of resource selection. The number of observed locations from resident animals in Pantanal within increasing bin ranks was counted, and the observed selection was then compared to the predicted selection in each bin. To assess the relationship between bin ranks and the number of observed locations, we used 2 alternative analyses: 1) Spearman's rank correlations (Boyce et al. 2002), considering model validation to be high when  $r > 0.6$ , and 2) simple linear regression (Howlin et al. 2004). The slope of the regression model, with the predicted selection as the predictor of observed selection, is a measure of the predictive ability of the model. When the slope is not significantly different from zero, the predictive abilities of the model are unacceptable. When the slope is positive, the predictive abilities of the model are considered acceptable, and we can assume that the resulting probability is "proportional to the probability of use" (Manly et al. 2002; Howlin et al. 2004; Johnson et al. 2006).

We used the better-validated model from Iberá to develop a rasterized probability map for anteaters in Pantanal using the Raster Calculator tool in ArcGIS 10.3. We defined 5 equally ranked bins (20% each) as 1) poor, 2) low, 3) moderate, 4) good, and 5) high probability of occurrence of giant anteaters (Di Blanco et al. 2015).

*Home-range estimations.*—We estimated home-range size for maximum periods of 1 year for each radiotagged giant anteater in both sites ( $n = 9$  in Iberá;  $n = 10$  in Pantanal) using the kernel density estimation (KDE) method with a least squares cross-validation smoothing parameter (Worton 1989). Data on Pantanal animals were collected for a maximum period of 1 year; therefore, we used the same data set used for analyses of habitat selection ( $107 \pm 25$ , mean  $\pm SE$  locations per individual). Reintroduced animals in Iberá were monitored for variable periods of time, often for more than 1 year. As home-range estimates are dependent on time, for estimation of annual home ranges in Iberá, we discarded locations beyond a period of 1 year for each individual, performing analyses with a mean ( $\pm SE$ ) of  $40 (\pm 5)$  locations per animal. We estimated 95% KDE using ArcGIS through the GME and the R environment. To assess differences between sites and sexes, their possible

interaction, and to account for the relatively small sample size, we used permutation analyses of variance (PERM ANOVAs), performed using the *ImPerm* package (Wheeler and Torchiano 2016). We used the R software for all statistical procedures.

## RESULTS

*Pantanal habitat models.*—We found that models with random intercepts and coefficients improved model fit given the variation of responses in habitat selection among Pantanal giant anteaters, while behavior seems to be similar between the sexes (Supplementary Data SD2). Different combinations of predictor covariates were included in the better-ranked models, according to their relative AIC weight (Table 2). During the dry season, habitat type seemed to be the most important predictor variable, which was included in all models with higher relative weight. DFE was the most important covariate for the wet season and both DFE and habitat type were the best predictors of habitat selection during activity and resting periods (Table 2). Considering 90% CIs as indicator of selection after model averaging, it is clear that the DFE was the most important predictor variable describing habitat selection. Animals preferred places not far from forests in both seasons and both when active and resting (Table 3). Animals also selected places near human settlements, but only during the wet season. Floodplains were avoided during the dry season and for resting periods, while they were not avoided or selected during the dry season and during activity. Active animals seemed to be more selective of the type of habitat, avoiding forests and selecting positively open savannas (Table 3).

*Validation of the Iberá habitat model at Pantanal.*—The general model based on adult animals at Iberá was poorly validated by the dry season data (June–November) of wild animals from Pantanal (Spearman's rank validation = 23%; regression  $F_{1,18} = 0.95$ ,  $P = 0.343$ ) when we discarded floodplains and locations within them. Using the wet season data from the Pantanal, Spearman's rank showed a higher correlation of 52%, and the regression test was near significance ( $F_{1,18} = 3.85$ ,  $P = 0.065$ ; Table 4). When we validated the general model from Iberá with the dry season locations from the Pantanal, but this time considering non-flooded floodplains as available open savannas, Spearman's correlation became slightly higher (53%) and, according to regression, validation was acceptable ( $F_{1,18} = 7.6$ ,  $P = 0.013$ ). The validation of the model from active animals in Iberá was always unacceptable. However, the model from inactive animals was highly validated (Table 4). The best-validated model from inactive giant anteaters (Spearman's rank validation = 77%; regression  $F_{1,18} = 23.69$ ,  $P = 0.0001$ ; Table 4), applied to the Pantanal study site, showed that 38% the landscape has a good-to-high likelihood for giant anteaters (Fig. 2).

*Home-range comparisons between sites.*—A 2-way permutation ANOVA showed a statistically significant interaction between site and sex on home-range size ( $F_{1,15} = 5.69$ ,  $P = 0.0279$ ). Separate analyses for each sex showed that the home ranges of Iberá males were larger ( $32.50 \pm 7.64$ ) than those of Pantanal males ( $14.07 \pm 1.97$ ;  $F_{1,5} = 4.02$ ,  $P = 0.0288$ ),

**Table 2.**—Data sets and corresponding best-ranked competing models (fixed effects) of habitat selection by wild giant anteaters (*Myrmecophaga tridactyla*) in the Pantanal. Sample effort is described through the mean number of locations per individual  $\pm SE$  and the total number of locations and individuals in each data set. Models totaling  $\geq 95\%$  of total AIC weight, corresponding  $\Delta AIC$  scores, and the number of estimable parameters ( $k$ ) are reported. AIC = Akaike Information Criterion; DFE = distance to forest edge; DHS = distance to human settlements; DWP = distance to permanent water ponds.

Data set	Mean loc./indiv. $\pm SE$	$N$ Locations/ $N$ individuals	Fixed parameters	$k$	$\Delta AIC$	Weight ( $w_i$ )
Dry season	69.7 $\pm$ 9.9	697/10	Habitat type + DFE + DHS	16	0.00	0.488
			Habitat type + DFE + DHS + DWP	17	1.48	0.232
			Habitat type + DFE	15	2.17	0.165
			Habitat type + DFE + DWP	16	3.13	0.102
Wet season	91.5 $\pm$ 19.3	336/4	DFE + DHS	11	0.00	0.686
			DFE	10	2.33	0.214
			Habitat type + DFE + DHS	12	4.75	0.064
Activity	58.9 $\pm$ 10.6	589/10	Habitat type + DFE	15	0.00	0.579
			Habitat type + DFE + DWP	16	1.38	0.290
			Habitat type + DFE + DHS + DWP	17	3.32	0.110
Inactivity	47.4 $\pm$ 14.4	474/10	Habitat type + DFE	15	0.00	0.395
			Habitat type + DFE + DWP	16	1.59	0.178
			Habitat type + DFE + DHS	16	2.00	0.145
			Habitat type + DFE + DHS + DWP	17	3.23	0.079
			DFE + DHS	15	3.31	0.075
			DFE	14	3.54	0.067
			DFE + DWP	15	5.10	0.031

**Table 3.**—Coefficients of explanatory variables (with lower and upper 90%  $CI$ s) from model averaging in resource selection functions of giant anteaters (*Myrmecophaga tridactyla*) in the Pantanal. Continuous covariates (distances) were rescaled from actual distances to 0–1 parameters. Bold and \* indicate values where 90%  $CI$ s do not overlap zero.

Data set	Intercept	Habitat type— Forest	Habitat type— Grassland	Habitat type— Open savanna	Habitat type— Floodplains	Distance to forest edge	Distance to human settlements	Distance to permanent water ponds
Dry season	−1.534 (−4.043, 0.975)	−0.181 (−0.453, 0.091)	−0.483 (−1.625, 0.658)	0.127 (−0.191, 0.445)	<b>−0.840*</b> (−1.220, −0.460)	<b>−4.468*</b> (−6.650, −2.286)	−1.871 (−7.006, 3.263)	1.041 (−2.280, 4.361)
Wet season	0.406 (−2.272, 3.084)	0.877 (−1.224, 2.978)	−1.591 (−9.337, 6.155)	0.288 (−0.897, 1.473)	0.920 (−0.523, 2.363)	<b>−2.300*</b> (−3.282, −1.317)	<b>−10.606*</b> (−16.666, −4.546)	
Activity	−2.205* (−3.673, −0.737)	<b>−0.315*</b> (−0.616, −0.015)	−0.220 (−1.418, 0.977)	<b>0.567*</b> (0.235, 0.900)	0.074 (−0.278, 0.427)	<b>−4.789*</b> (−6.923, −2.654)	−0.739 (−5.986, 4.508)	0.711 (−1.748, 3.169)
Inactivity	−2.374* (−4.172, −0.577)	0.479 (−0.514, 1.473)	−3.716 (−12.894, 5.462)	−0.885 (−1.874, 0.104)	<b>−1.081*</b> (−1.985, −0.179)	<b>−2.120*</b> (−3.330, −0.910)	0.839 (−5.034, 6.711)	−0.738 (−2.871, 1.396)

**Table 4.**—Validation assessments by Spearman's rank correlations and simple linear regressions of resource selection models from giant anteaters (*Myrmecophaga tridactyla*) at Iberá, using data from Pantanal. Bold and \* indicate statistical significance ( $\alpha = 0.05$  for simple regression;  $r > 0.6$  for Spearman's rank correlation).

Data set model at Iberá	Data set validation at Pantanal	$N$ Individuals/locations in validation data set	$Rho$ -value Spearman's correlation	$F_{1,18}$ -value linear regression	$P$ -value linear regression
Adults, general	Wet season, excluding floodplains	4/293	0.52	3.85	0.065
	Dry season, excluding floodplains	10/637	0.23	0.95	0.343
	Dry season, floodplains as open savannas	10/697	0.53	7.60	<b>0.013*</b>
Adults, active	Active, excluding floodplains	10/482	−0.53	0.57	0.459
	Active, dry season, excluding floodplains	10/365	−0.70	0.64	0.434
	Active, dry season, floodplains as open savannas	10/413	0.34	1.10	0.308
Adults, inactive	Inactive, excluding floodplains	10/448	<b>0.61*</b>	11.53	<b>0.003*</b>
	Inactive, dry season, excluding floodplains	10/272	0.58	8.98	<b>0.008*</b>
	Inactive, dry season, floodplains as open savannas	10/284	<b>0.77*</b>	23.69	<b>0.0001*</b>



whereas home ranges of females were similar in both places ( $9.75 \pm 1.74$  for Iberá and  $9.62 \pm 2.00$  for Pantanal;  $F_{1,10} = 0.002$ ,  $P = 0.9216$ ; Fig. 3).

## DISCUSSION

Resource abundance and distribution are primary factors determining habitat selection. It is important to understand why a species selects a particular area or any of its components (e.g., for feeding, refuge, or reproduction sites), which may differ in productivity and relative suitability (Johnson 1980). In this study, we compared habitat selection of reintroduced and resident giant anteaters in similar though distant regions of South America. Reintroduced and resident animals showed some degree of similarity in spatial patterns, suggesting that some features of the landscape, mainly forest patches, are very important for giant anteaters as suggested in our 1st hypothesis.

Pantanal animals avoided forests and selected open savannas during their activity and avoided floodplains for resting

periods (Table 3). This pattern also was found in other studies at Pantanal, where giant anteaters used open habitats to feed or travel and forested areas for resting periods. When resting, their capacity to thermoregulate decreases and they may be more vulnerable to predators (Camilo-Alves and Mourão 2006; Mourão and Medri 2007). It is remarkable that even when avoiding forests, animals always selected places not far from this habitat type, suggesting the important role of forests as potential refuges or protection against predation.

The positive selection of places near forests by Pantanal animals also supported our 1st hypothesis and was similar to what was found for reintroduced animals in Iberá (Di Blanco et al. 2015). However, the avoidance of forests during periods of activity and the lack of selection of this habitat type for resting was unexpected. The positive selection of forests by Pantanal animals seems to be less clear than that by reintroduced animals in Iberá. Pantanal animals avoided forests during activity periods and they neither avoided nor selected forests for inactivity periods or across seasons. Reintroduced animals showed a more defined selection for forests, except during activity periods (Di Blanco et al. 2015). This difference in behavior can be attributed to reintroduced animals selecting the most suitable habitat for resting but not necessarily during their activity, as their foraging experience and abilities may be impaired due to their experience in captivity. On the other hand, differences between sites may better explain this variability between reintroduced and resident populations. One of the main differences between Iberá and the Pantanal is the climate. Iberá is near the southern limit of the historic distribution of the giant anteater, which is likely limited by the low temperatures during the winters (higher seasonality). Considering the limited ability of giant anteaters to control their body temperatures (McNab 1984), forests probably play a more important role as thermal protection in Iberá. In addition, continuous forests were the least extensive habitat type in Iberá (< 5%), whereas they were dominant in Pantanal (40–50%; Table 1). When a resource is highly preferred, but it is also highly available, there will be no strong evidence of selection for that resource. The weak selection pattern by giant anteaters in Pantanal also was reported in other studies (Medri and Mourão 2005; Desbiez and Medri 2010), where the species used different habitat types roughly according to their availability. In accordance to our prediction, the higher availability of forests in Pantanal may explain the variable selection and the avoidance of this habitat type by resident giant anteaters.

Wild animals from Pantanal seemed to prefer places not far from human settlements during the wet season, showing, during this season, the opposite pattern to the one we expected. This association may be related to the location of human settlements in higher terrain to avoid flooding. One of the main differences between study sites is that animals in Iberá had the option to select areas without cattle, whereas they had no such option in Pantanal. The reintroduced population avoided areas dedicated to livestock production. This was probably related to the extremely open vegetation structure resulting from cattle ranching, in addition to the frequent fires, the regular use of dogs, and

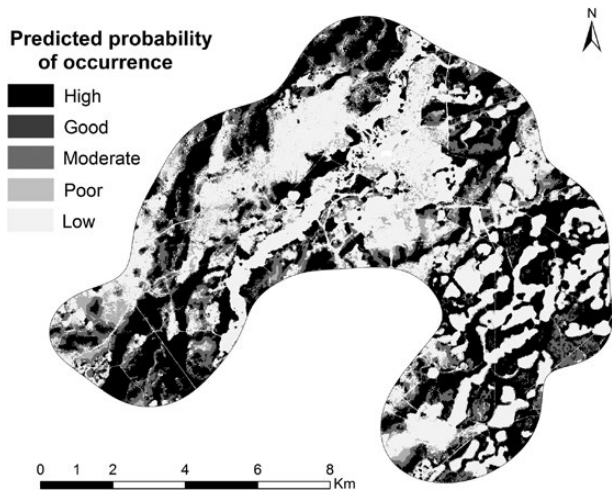


Fig. 2.—Probability of occurrence of giant anteaters (*Myrmecophaga tridactyla*) in the Pantanal study site according to the best-validated model based on giant anteaters at Iberá during inactive periods.

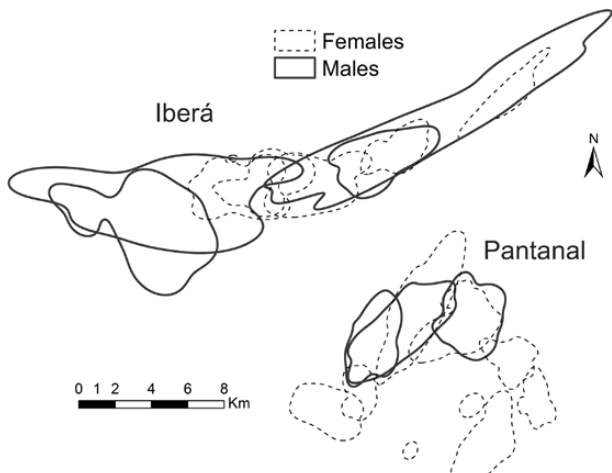


Fig. 3.—Individual home ranges of female and male giant anteaters (*Myrmecophaga tridactyla*) in Iberá and Pantanal, estimated as the 95% isopleth of the kernel density function.



poaching, commonly associated with this activity in Iberá. In this region, strict conservation areas without traditional cattle management or with proper forest cover seem to be a requisite for the successful reintroduction and persistence of giant anteaters (Di Blanco et al. 2015). However, in Pantanal, human settlements are scarce and hunting is uncommon among the local people (Desbiez et al. 2011), with just a few farm houses where animals can walk nearby without being disturbed. In addition, the lack of roads complicates human access to the area, and forests are abundant as refuge. This may suggest that habitat selection by giant anteaters in the Pantanal study site depended more on the search for food and intraspecific interactions than on the negative effects of cattle management or other human impacts.

When making comparisons among sites, some resources may be unavailable in 1 site, making the comparisons difficult. Floodplains became unavailable for most terrestrial species during part of the wet season, which can explain why validation of the general model from Iberá in Pantanal was only acceptable during the dry season months and when considering the temporary, non-flooded floodplains as available. Iberá models were poorly validated in Pantanal when excluding this habitat type during the dry season, but were near acceptable during the wet season (Table 4). These results suggest that availability of habitats changes drastically in the Pantanal study site across the year, and this is reflected in the animals' behavior. It is therefore important to carefully consider the possible seasonal change in habitat availability when constructing resource selection models, as well as for their validation.

In Iberá, giant anteaters used more habitats during periods of activity, showing a less-evident pattern of habitat selection than when resting (Di Blanco et al. 2015). Animals in Pantanal were more selective during activity periods and their locations showed the worst validation of the predictive model from Iberá ( $\leq 34\%$  of correlation), compared to the same animals when they were resting (highly significant with correlations of 58–77%). Activity is mainly dedicated to feeding purposes. Differences in food distribution between sites may explain the low validation of activity models, whereas the common use of forests for resting explains the higher validation for inactivity models. The predictive ability of our resource selection models for giant anteaters in Pantanal might be improved with the addition of covariates on food distribution, if these were available.

Home-range size was different between sites, but, in partial disagreement with our 2nd hypothesis, only males accounted for these differences. Males may respond differently than females to differences in resource distribution between sites (e.g., inter-male competition for food, mates, or refuge). It has also been suggested that home-range size of females may depend more directly on food availability, whereas for males it may depend on the availability and distribution of females (Powell 2000). The population at Iberá was recently reintroduced, and may not yet have reached its carrying capacity. The higher densities of males in Pantanal, and consequently higher level of social interactions, can restrict their movements compared to Iberá. Long-term monitoring of reintroduced animals to estimate density, home-range overlap, and territoriality can clarify these questions.

Resource selection models are rarely validated with data from landscapes independent of those from which the models were built (Wiens et al. 2008). This lack of geographic validation poses an obstacle to understanding the spatial as well as the temporal repeatability and applicability of resource selection patterns for a given species (Coe et al. 2011). In this study, we compared and validated models of habitat selection from reintroduced giant anteaters in the Iberá ecoregion of Argentina with data from wild animals in a similar though distant ecoregion in Brazil. We have shown that while habitat selection was not strong in the Pantanal, the validation of models developed in a physiognomically similar location allowed us to highlight and understand the importance of certain habitat and species attributes, particularly the role of forests for giant anteaters. In Iberá, only 4% of the landscape has a good-to-high probability of selection, mainly concentrated in the forest patches and their proximity (Di Blanco et al. 2015). In contrast, around 50% of the area under study in Pantanal has a good-to-high probability of selection (Fig. 3). Model validation, especially when making spatial predictions, should be considered an essential element and step in the RSF modeling process (Johnson et al. 2006). Model validation in independent areas should be encouraged to assess whether attributes or resources selected by a population can be generalized for the species, even when those are highly abundant or available. This also may be a useful tool to assess whether reintroduced populations present similar patterns of resource selection as those of resident populations, and to predict which habitats are essential for the successful reintroduction of populations.

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#### SUPPLEMENTARY DATA

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

**Supplementary Data SD1.**—Habitat types description and mapping. The description of the habitat types and their differences between Pantanal and Iberá are detailed and shown with images. Mapping techniques are also described.

**Supplementary Data SD2.**—GLMM—Random structure selection. Here is described how the random structures of models were selected. A table showing resulting best random structures used for modeling are also reported.

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