



Habitat selection in reintroduced giant anteaters: the critical role of conservation areas

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Habitat selection by the 1st reintroduced population of giant anteaters (*Myrmecophaga tridactyla*) was studied at Iberá Nature Reserve (northeastern Argentina), a subtropical region of wetlands, grasslands, and forests, with properties dedicated to nature conservation or livestock production. Eighteen animals were released and radiotracked between 2007 and 2012 for periods of 6–46 months, producing 1,181 locations. The effect of land use was assessed using chi-square tests. Resource selection functions were used to assess habitat selection at 2 spatial scales using as covariates habitat type (grassland, open savanna, closed savanna, and hygrophilous forest), distance to forest edge, and distance to a main road. Habitat selection was modeled for different ages (juveniles and adults), activity (resting or active), and seasons (summer, transition, and winter) and was validated with individuals previously excluded from our analysis. Anteaters strongly selected areas dedicated to nature conservation. Adults showed higher model fit. Hygrophilous forest was positively selected and open savanna was avoided. Anteaters rested almost exclusively in forests. While active they increased the use of other habitats, except for open savanna. Grasslands were most used during the winter season, probably because they provide a constant food source and better cover than savannas. Even though < 4% of the landscape was covered by forests, this habitat proved to be important for giant anteaters. Deforestation and traditional cattle management may have caused the local extinction of the species at Iberá. Establishment of strict conservation areas in nonflooded areas combined with proper management of forests and livestock may be essential for the long-term survival of reintroduced populations in Iberá and similar regions.

Se estudió la selección de hábitat de la primera población reintroducida de osos hormigueros del mundo en la Reserva Natural Iberá (NE de Argentina), una región subtropical dominada por esteros, pastizales y bosques, en propiedades dedicadas a la conservación de vida silvestre o a la producción ganadera. Se liberaron 18 animales que fueron monitoreados a través de radiotelemedría durante los años 2007–2012 por períodos de 6–46 meses, produciendo 1.181 localizaciones. El efecto del uso de la tierra fue evaluado con pruebas de chi cuadrado. Para evaluar el uso de hábitat a dos escalas espaciales se utilizaron funciones de selección de recursos (FSR), utilizando como variables el tipo de hábitat (malezales, sabanas, bosques abiertos y bosques higrófilos), la distancia al borde del bosque higrófilo (DBBH) y la distancia a una ruta principal (DR). Se generaron modelos de selección de hábitat para diferentes edades (adultos y juveniles), actividad (en actividad o reposo) y estaciones (verano, transición e invierno), que fueron validados con individuos previamente excluidos de los análisis. Los osos hormigueros seleccionaron fuertemente las áreas dedicadas a la conservación de la naturaleza. Los adultos mostraron un mejor ajuste a los modelos. Los bosques higrófilos fueron positivamente seleccionados y las sabanas evitadas. Los osos hormigueros descansaron casi exclusivamente en bosques higrófilos. En los períodos de actividad incrementaron el uso de otros hábitats, exceptuando las sabanas. Los malezales fueron utilizados sobre todo durante el invierno, probablemente debido que proveen recursos alimenticios de forma más constante y mejor cobertura que las sabanas. Aunque sólo < 4% del paisaje estuvo cubierto por bosques higrófilos, este tipo de hábitat es importante para el oso hormiguero. La deforestación y

el manejo ganadero tradicional pueden haber sido causantes de la extinción local de esta especie en Iberá. El establecimiento de áreas de conservación estricta en áreas no inundables combinado con un manejo apropiado de los bosques y el ganado puede ser esencial para la supervivencia a largo plazo de poblaciones reintroducidas en Iberá y regiones similares.

Key words: activity, cattle management, habitat use, *Myrmecophaga tridactyla*, protected areas, seasonality, thermoregulation, vegetation cover

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Reintroduction of endangered species is becoming a common activity within the conservation agenda (Ewen et al. 2012). Knowing which habitat conditions are needed to sustain a population is critical for the success of a reintroduction project (Armstrong and Seddon 2007). Resources positively selected by a species could indicate favorable conditions for its long-term survival, while avoided resources may reflect negative conditions (Manly et al. 2002).

Animals seem to select habitat in a hierarchical fashion. Johnson (1980) described 4 spatial scales or “orders of selection.” The 1st order corresponds to the distribution of a species; the 2nd order corresponds to where animals establish their home ranges; the 3rd is the selection of habitats or resources within home ranges; and the 4th order is the selection of specific resource items. Reintroduced animals in the process of establishing their home ranges can provide valuable information for understanding which factors determine patterns of 2nd and 3rd order of selection.

The giant anteater (*Myrmecophaga tridactyla*) is a widely distributed species, listed as “Vulnerable” in both the Red List of Threatened Species (IUCN 2013) and the Argentinean Red List (Superina et al. 2012). Across its range, *M. tridactyla* occupy diverse habitat types including grasslands, savannas, and forests (Gardner 2007).

This species, as other members of the superorder Xenarthra, has a lower basal metabolic rate and body temperature than other mammals of similar size (McNab 1985). For this reason, the presence of adequate cover from extreme temperatures might be a key factor determining habitat use by giant anteaters. Vegetation cover may also protect animals from being detected by predators. Cover could thus be an important determinant of anteaters’ fitness, for both thermal protection and antipredator defense.

Patterns of habitat use by giant anteaters may depend on activity, favoring open areas to forage and closed areas to rest (Camilo-Alves and Mourão 2006; Mourão and Medri 2007). They can increase forest use for both active and resting periods during the coldest or hottest days (Camilo-Alves and Mourão 2006), suggesting that habitat selection may also change with extreme temperatures and seasonality.

During the last 2 centuries Corrientes Province experienced the worst process of defaunation in Northern Argentina. Five species of mammals—giant anteater, jaguar (*Panthera onca*), giant otter (*Pteronura brasiliensis*), collared peccary (*Pecari tajacu*), and South American tapir (*Tapirus terrestris*)—and 2

of large birds—red-winged macaw (*Ara chloroptera*) and bare-faced curassow (*Crax fasciolata*)—became locally extinct, and the regional endemic glaucous macaw (*Anodorhynchus glaucus*) became globally extinct (Parera 2004; Canevari and Vaccaro 2007; Chebez 2008a, 2008b). Other large mammals like the marsh deer (*Blastocerus dichotomus*), the pampas deer (*Ozotoceros bezoarticus*), and the maned wolf (*Chrysocyon brachyurus*) became very scarce (Schaller and Tarak 1976). Regarding the giant anteater, several authors refer to the historical presence of the species in Corrientes Province and its extinction around the middle of the 20th century (D’Orbigny 1945; Fabri et al. 2003; Pérez Jimeno and Amaya 2007; Chebez and Cirignoli 2008). A longer history of European colonization than neighboring provinces, combined with a cattle ranching tradition based on the frequent use of fires and dogs, and widespread commercial/subsistence hunting until the 1970s appear as the potential causes for this defaunation process. When Iberá Nature Reserve (INR) was established by law in 1983, provincial park-rangers started to enforce hunting prohibitions, remnant wildlife populations recovered, and several authors proposed the reintroduction of extirpated fauna (Parera 2004; CLT 2007). Following this recommendation, in 2006 the government of Corrientes and The Conservation Land Trust (CLT) started the 1st project in the world aimed to restore an extinct population of giant anteaters (Jiménez Pérez 2013a). The first 2 animals were released in 2007 and further 31 animals have been released since then in an up-to-now successful effort (Jiménez Pérez 2013a).

The aim of this study is to describe habitat selection by the 1st reintroduced population of giant anteaters in order to identify critical factors that may hamper long-term survival for this and other populations of the species.

MATERIALS AND METHODS

Study site.—The INR is a 13,000 km² multiple use protected area (Canziani et al. 2003; Fig. 1) that includes a diverse mosaic of habitats. Currently, 40% of this area (5,530 km²) comprises public lands that have been declared a Provincial Park, a strict conservation area. This Park is made up of permanently flooded marshlands surrounded by upland ecosystems under private property and with very light conservation policies and enforcement. 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

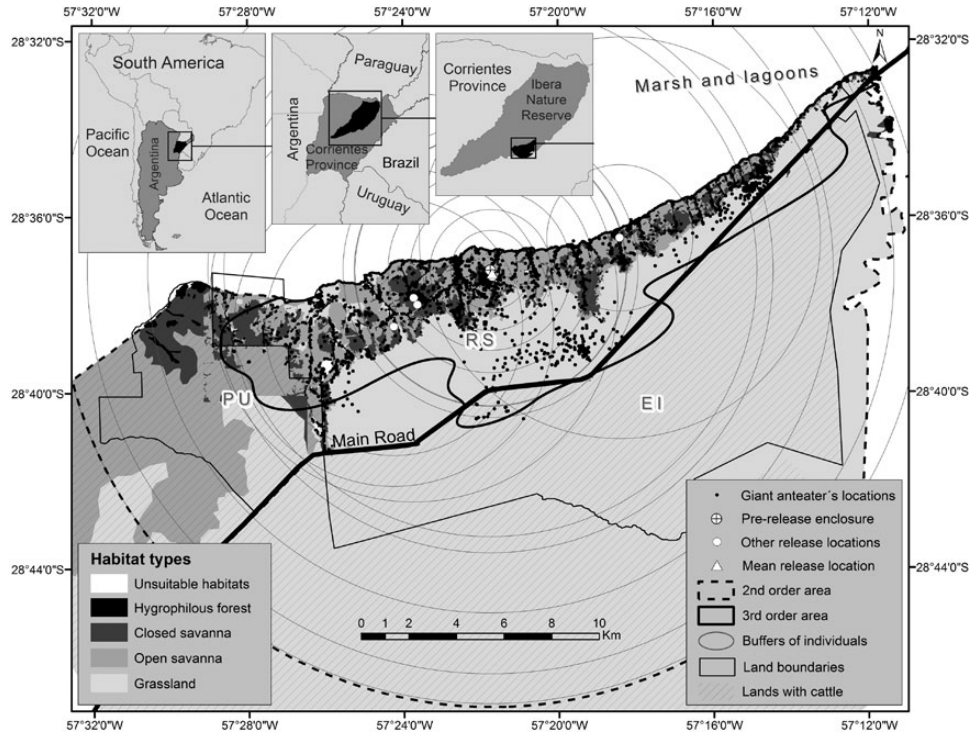


Fig. 1.—Study site, giant anteater (*Myrmecophaga tridactyla*) locations and release locations, scales of analysis, and references of their definitions.

months (January–February—[Neiff and Poi de Neiff 2006](#)). The most common land use in private properties within the INR is extensive cattle and sheep ranching, either in large ranches (*Estancias*, 20–200 km²) or in small- to medium-sized grouped properties (*Parajes*, 1–20 km²) inhabited by their owners and families. Within this framework of private properties included inside INR, CLT holds 1,500 km² of nature reserves dedicated to nature conservation and ecological restoration ([CLT 2007](#)).

Giant anteaters were reintroduced in one of such reserves: Rincón del Socorro (RS), a 124 km² property owned by CLT, located in the south-eastern portion of the INR ([Fig. 1](#); 28°39'S, 57°23'W). RS was a typical cattle ranch under high grazing pressure until 2002, when it was acquired by CLT and livestock was removed. This property serves as a strict conservation area where hunting is prohibited and controlled, livestock is absent, and there is a policy of limited fires in small patches that avoids regular burning of the whole property. To the east, RS limits with the Iberá lagoon where, in the opposite margin, is located the village of Colonia Carlos Pellegrini (< 1,000 inhabitants). To the west of RS is Paraje Uguay (PU), where around 30 families live on sparse and dispersed settlements within small ranches (< 20 km²) dedicated to livestock production—cattle (*Bos taurus*), sheep (*Ovis aries*), and horse (*Equus caballus*)—under high densities (1.3–5.5 livestock/ha) for regional standards ([Fig. 1](#)). Free-ranging dogs are abundant and poaching is not strictly controlled. People within PU hunt wild animals for meat (e.g., vizcacha, *Lagostomus maximus*), meat and leather (e.g., capybara, *Hydrochaeris hydrochaeris*), or for predator control (e.g., foxes *Cerdocyon thous* and *Lycalopex gymnocercus*—[Di Bitetti et al. 2009](#)). To the southeast, a dirt road separates RS from Estancia

Iberá (EI), a 170 km² property, also owned by CLT, but leased for cattle production under strict conditions: carrying capacity is set at 0.29 animals/ha or around 50% of the recommended cattle density for this habitat, the use of dogs forbidden, and hunting is controlled ([Perea Muñoz et al. 2010](#)).

We classified the main terrestrial habitats into 4 types ([Table 1](#)). 1) The grassland is a seasonally flooded habitat known locally as Malezales, dominated by 1.5–2 m high *Andropogon lateralis*. This habitat type covers the southern portion of RS and PU, and almost the whole surface of EI ([Fig. 1](#)). 2) The open savanna is a wooded habitat typical of the Espinal ecoregion dominated by the caranday palm (*Copernicia alba*) and 2 legume trees (*Prosopis affinis* and *Acacia caven*) very sparsely distributed in space over a short to medium height herbaceous layer. 3) The closed savanna is also characterized by the same species as the open savanna, but including small forest patches (< 200 m²) and bushes embedded in an herbaceous layer. 4) The hygrophilous forests, along small and temporary streams, form a continuous canopy that reach 15–20 m in height and include a diverse array of trees typical of the Atlantic Forest ([Tressens et al. 2002](#)). Hygrophilous forests are usually surrounded by both types of savannas, and these 3 habitat types are concentrated in the north of RS and PU ([Fig. 1](#)).

Land use affects the final expression of these habitats. Livestock makes savanna habitats more open and with less trees and bushes in PU than in RS. Herbaceous vegetation is significantly shorter and with lower cover in both grasslands and savannas dedicated to livestock production, when compared to those under strict conservation management (see [Supporting Information S1](#)).

Table 1.—Summary of the 4 main habitat types, number of locations recorded in each habitat and their relative contribution in area and percentage in the study site, according to spatial scales. Habitat classification was based on vegetation structure (canopy cover and grass understory).

Habitat type	Vegetation structure	Number of locations	2nd-order area (km ²)	2nd-order percentage (%)	3rd-order area (km ²)	3rd-order percentage (%)
Hygrophilous forest	Dense canopy cover, grass understory absent.	376	7.25	1.34	5.59	4.79
Closed savanna	Medium canopy cover, bushes and short–medium grass understory.	344	28.47	5.28	19.52	16.72
Open savanna	Open canopy cover, short–medium grass understory.	141	74.73	13.86	31.39	26.89
Grassland	No trees or bushes, tall grass in nongrazed areas, generally short–medium grass in areas with cattle.	320	428.78	79.52	60.23	51.70

Study animals and location data.—From October 2007 to December 2013, 31 giant anteaters (18 males and 13 females) were released in RS to reestablish the species in the area. Animals were released according to their availability, starting with 2 animals released in 2007 up to 7 in 2012 (I. Jiménez Pérez, pers. obs.). Further releases to this site were stopped in 2013 based on survival and reproductive data that pointed to the long-term sustainability of the reintroduced population (Jiménez Pérez 2013b).

All animals were fitted with harnesses equipped with very high frequency transmitters with activity and mortality sensors (Telonics, Mesa, Arizona—see Di Blanco et al. 2012). Released animals had different ages (from 1 up to around 8 years old) and origins from the Argentinean Chaco region (Jiménez Pérez 2013b). Twenty-two of them were rescued very young (< 1–10 months old) from local people that captured them in the wild. These animals were captive-reared in CLT facilities until they reached the age and size to be radiomarked and released (12–18 months old or > 18 kg). Six adult animals (> 3 years old—Redford and Eisenberg 1992) came from zoos or government facilities in different provinces, and 3 wild animals were rescued after being injured by hunters or road accidents and released after recovery.

Individuals were followed for varying periods. We only used data from individuals that were monitored for a minimum of 6 months ($n = 18$ individuals, $\bar{X} \pm SD = 18.94 \pm 11.43$ months). Hard releases were used during the first 2 years of the project and with rehabilitated wild adult animals. In these cases ($n = 6$), anteaters were translocated and released in different sites within RS (see Fig. 1) after spending a short period in a 0.5-ha acclimatization pen. Twelve animals were transported to a 7-ha prerelease pen sited in a remote area within RS (see Fig. 1), where they spent 7–30 days until the gates were open and animals could leave by themselves. While in the prerelease pen and for several weeks after leaving it, anteaters received supplementary food that was gradually removed, depending on the general condition of the animal. Management of all animals has been conducted under Argentinian and provincial permits and in accordance with the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

Free-ranging anteaters were located by “homing in,” following the radio signal until the animal was actually seen or heard, to avoid the error generated by triangulation (Samuel and Fuller 1994). This also allowed us to precisely associate the location to a habitat type. Since giant anteaters have a developed sense of smell, we approached the focal animals always downwind and as silently as possible to avoid disturbing their ongoing behavior. The activity sensor indicated whether the animal was active or inactive before approaching it to record its location. When the animal was inactive or sleeping we removed the antenna of the receiver to confirm that the animal was within 10 m (without the antenna animals located > 10 m usually cannot be detected), so we could be accurate about the location of the animal without the need to visually observe it. Locations were sampled around the clock, as frequently as once per hour in 24-h periods, but at least once every 30 days. The continuous observation of a focal individual for several hours within a single day resulted in the eventual detection of the observer by the focal animal, which probably affected the animal’s normal behavior. To address this potential bias and to ensure independence of continuous location data, we only used the 1st location within a 24-h period. The number of locations and individuals considered for analysis are detailed in Table 2.

Scales of analyses.—Habitat selection was studied at 2 spatial scales that roughly correspond to Johnson’s (1980) 2nd- and 3rd-order resource selection. We followed individuals to identify a set of used resources, but assessed availability at the population level (Design II approach) assuming that availability of resources did not vary during the study period (Manly et al. 2002). We defined a 2nd order of selection area by the overall displacement of the individuals, assuming that this represents the available area where they could potentially establish their home ranges. This area was defined as the sum of buffers around the individual release locations, each buffer representing a circle with radius equal to the maximum displacement by an individual (Fig. 1).

Because of the differences in number of locations collected per individual, the 3rd-order selection area was defined as the range estimated for the population as a whole, including all locations of individuals monitored for at least 6 months, but excluding locations acquired within 30 days after release

Table 2.—Data sets and corresponding best-ranked models. Sample effort is described through the mean number of locations per individual \pm *SD* and the number of locations and individuals (number of locations/number of individuals) for training and testing data. Model fit is indicated by the explained deviance and validation score. AIC = Akaike Information Criterion; DFE = distance to forest edge; DMR = distance to the main road.

Data set	Mean loc./ indiv. \pm <i>SD</i>	Training data ^a	Testing data ^a	Order of selection	Best-ranked model	Δ AIC 2nd best model ^b	Dev. explained by model (%) ^c	Spearman's rank validation
All individuals (<i>n</i> = 18)	66 \pm 46	980/14	217/4	2nd	Habitat type + DFE + DMR	-66.0	24.03	0.90
				3rd	Habitat type + DFE + DMR	-22.3	15.63	0.51
Adults (<i>n</i> = 9)	84 \pm 54	575/7	128/2	2nd	Habitat type + DFE + DMR	-42.9	39.02	0.94
				3rd	Habitat type + DFE + DMR	-10.5	33.56	0.91
Juveniles (<i>n</i> = 10)	47 \pm 27	403/7	89/2	2nd	Habitat type + DFE + DMR	-26.8	9.35	0.72
				3rd	Habitat type + DFE + DMR	-8.9	3.04	0.41
Adults-active (<i>n</i> = 9)	36 \pm 37	277/7	50/2	3rd	Habitat type + DFE + DMR	-9.5	23.25	0.72
Adults-inactive (<i>n</i> = 9)	41 \pm 26	294/7	72/2	3rd	Habitat type + DFE	-1.9 ^d	39.50	0.87
Adults-winter (<i>n</i> = 8)	29 \pm 26	174/6	54/2	3rd	Habitat type + DFE	-1.0 ^d	21.86	0.78
Adults-transition (<i>n</i> = 9)	27 \pm 25	202/7	40/2	3rd	Habitat type + DFE	0.9 ^d	31.03	0.81
Adults-summer (<i>n</i> = 9)	26 \pm 14	199/7	34/2	3rd	Habitat type + DFE + DMR	-17.5	35.03	0.97

^aNumber of locations/number of individuals.

^b Δ AIC difference between the best-ranked model and the 2nd best-ranked model.

^cCalculated as $100 - ([\text{residual deviance} * 100]/\text{null deviance})$.

^dCompeting 2nd or 1st model in rank = habitat type + DFE + DMR.

(Fig. 1). Using the Geospatial Modelling Environment software (GME, Version 0.7.2.1—Beyer 2012), the population range was estimated 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).

We used field data and GIS to demarcate habitat types in ArcGIS 10.1 (ESRI 2010). We created a map of the different habitats of the study site using a 1 \times 1-m resolution image Ikonos 2008 (GeoEye Inc., Herndon, Virginia), including the 4 main habitat types and habitats not suitable for giant anteaters, such as marshes, lagoons, and human-transformed areas. We georeferenced field observations at boundaries between habitat types to improve the initial map. Habitats not suitable for the species were excluded from the potential range, and locations in those habitats (< 1% of locations) were therefore excluded from our analysis.

Data analysis.—Resource selection functions (RSFs) are functions proportional to the probability of use for a resource unit. They allow the assessment of predictor variables and provide an understanding of each variable's importance in resource selection by animals. The most common algorithm used in RSFs is a logistic regression through a generalized linear model approach comparing used locations to available locations (Manly et al. 2002). We compared anteater locations to a set of random "available" locations to determine the maximum-likelihood values of model coefficients (Johnson et al. 2006). We used R software (R Core Team 2013) for all statistical procedures. We used the Akaike Information Criterion (AIC—Burnham and Anderson 2002) with forward and backward model procedures including the complete set of covariates in order to select highest-ranked model for each data set using the package MASS (Venables and Ripley 2002). When the 2nd-ranked model had a Δ AIC > 4 units from the best model (Burnham and Anderson 2002), we only reported the best-ranked one. Models with AIC scores near (Δ AIC with an

absolute value of 0–2 units) a more parsimonious model containing one less variable should be closely inspected since the new variable may not be biologically relevant or meaningful (Burnham and Anderson 2002; Arnold 2010). This occurred in 3 of the model sets we studied. In these 3 cases, we reported the most parsimonious model, but indicated the structure of the competing model. We provide all candidate models as supplementary results. In any case, the importance of the covariates in the competing models was also assessed by an estimate of their confidence intervals (CIs; see below).

We used animals rather than their locations as the experimental unit (Aebischer et al. 1993). We weighted each animal according to the number of locations, estimating CIs from bootstraps, randomly selecting individuals and repeating the process 1,000 times. Bootstrapping resulted in more conservative lower 5th and upper 95th percentiles of 90% CIs (Thomas and Taylor 2006; Arnold 2010). We considered as selected (i.e., statistically significant) the covariate or category for which 90% CIs after bootstrapping did not include zero (0), avoiding less conservative *P* values and narrower CIs from the initial models.

Since release sites were nonrandomly located near forest areas, we modeled with RSFs the probability of occurrence using the distance to release location as a covariate. To do so, we first generated 2,000 and 5,000 random locations within 3rd- and 2nd-order selection areas, respectively (R. Nielson, Western EcoSystems Technology Inc., pers. comm.; but see Nielson et al. 2004). For each animal location we measured its distance to the release site, and for each random location, we measured the distance to a mean release site throughout the mean coordinates of each individual release location (Fig. 1). The distance to release site was an important predictor variable in this simple model after bootstrapping. We used the resulting coefficients (–0.0005 and –0.0002 for 2nd and 3rd order, respectively) to generate a new set of 5,000 and 2,000 random locations affected by these probabilities, which were

the availability locations used to develop the final models (see example in [Supporting Information S2](#)).

We defined 2 categorical covariates: habitat type (hygrophilous forest, closed savanna, open savanna, and grassland; [Table 1](#)) and land use (livestock production at PU and EI, and strict conservation at RS). We excluded land use as a covariate in the competing models because only 20 locations from 3 individuals were recorded in areas with cattle, 17 of which belonged to a single individual. For this reason, we assessed the differences in proportions of used versus available locations, between lands under livestock production and strict conservation at both scales, with chi-square tests ([Neu et al. 1974](#)) where expected values were corrected by the effect of release site.

We also included 2 continuous variables in RSF models: distance to forest edge (DFE), corresponding to the edge of hygrophilous forest, and distance to the main road (DMR). Before modeling we checked for multicollinearity inferred by Spearman's rank correlation $> |0.6|$ and variance inflation factor > 5 ([Menard 1995](#)), using the car package for the R environment ([Fox and Weisberg 2011](#)). We modeled habitat use at both spatial scales by age class (adults, juveniles, combined), as well as by activity (active, inactive), and across 3 seasons at the smaller spatial scale ([Table 3](#)). For this study, we divided the year in three seasons: winter (from May to August), summer (from November to February), and transition (March, April, September, and October). These seasons differ in mean temperature as well as other climatic variables that may affect giant anteater's metabolism and energy budgets.

We validated the models with independent individuals that were previously removed from the analysis ([Boyce et al. 2003](#); [Johnson et al. 2006](#)). We excluded a random sample of approximately 20% of the individuals that were later used as testing data. To avoid potential biases and for further subset validation, we randomly selected as testing data equal proportions of individuals from each sex and age class ([Table 3](#)). To validate models, we predicted the relative probability of selection of training data set and testing data set, and combined and classified all predictions into 10 quantile bins. The number of observed locations in each bin was counted and a Spearman's rank correlation to test the relationship between bin ranks and the number of observed locations within increasing bin ranks. We considered model validation to be high when $r > |0.7|$ ([Boyce et al. 2002](#)).

For both scales of selection, we constructed rasterized probability maps with the Raster Calculator tool in ArcGIS 10.1 ([ESRI 2010](#)), using each "selected" covariate coefficient included in the best-ranked model. We defined 5 equal ranked bins (20% each) as (1) poor, (2) low, (3) moderate, (4) good, and (5) high probability of occurrence of giant anteaters.

RESULTS

The areas for 2nd- and 3rd-order habitat selection were 539.23 and 116.73 km², respectively. The hygrophilous forests were the least extensive habitat type and the grassland the most extensive ([Table 1](#)). Buffers of individuals were highly overlapped, and the area estimated for 2nd-order selection was

comprised of the buffered area of 1 individual that included all others ([Fig. 1](#)).

Giant anteaters were practically absent from areas dedicated to livestock production at both scales of analysis (2nd order, $\chi^2 = 375.52$, $d.f. = 1$, $P < 0.0001$; 3rd order, $\chi^2 = 75.23$, $d.f. = 1$, $P < 0.0001$). As explained above, land use was further excluded from testing models due to the lack of locations in areas with livestock. The RSF model including the complete set of covariates was habitat type + DFE + DMR. The models including habitat type and DFE (and to lesser degree DMR) yielded the best fit to the observed data. All data sets models included the 2 first variables, but 3 including DMR did not reduce the AIC by > 2 units ([Table 2](#) and [Supporting Information S3](#) for details).

Models of only adult individuals explained a higher proportion of deviance and had higher validation scores ([Table 2](#)). The model that included all individuals for the 3rd order of selection showed relatively low model fit (16% of deviance explained) and low model validation ($r = 10.511$; [Table 2](#)). DMR was included in most of the best-ranked models; but bootstrapping results suggested no selection (90% CIs always included 0).

Patterns of habitat selection did not differ markedly between scales of analysis ([Fig. 2](#)). The hygrophilous forest was the most positively selected habitat type, the open savanna the most avoided, while the closed savanna and the grassland were not always selected. Juveniles did not select habitat types as markedly as adults ([Figs. 2b](#) and [2c](#)).

When compared to the closed savannas, inactive anteaters selected positively the hygrophilous forest and negatively open savannas. When active, they showed avoidance of open savanna but no preference for other habitat types ([Fig. 3a](#)). During the winter, giant anteaters seemed to be less selective, only avoiding the open savannas. The hygrophilous forest was selected positively during transition and summer seasons and the open savannas were avoided year-round. Anteaters showed a marked seasonal shift in the way they used the grassland, from no selection during winter and transition to complete avoidance during the summer ([Fig. 3b](#)). DFE was an important predictor of habitat selection ([Fig. 4](#)). This feature did not vary with animal activity ([Fig. 5a](#)) or seasonally ([Fig. 5b](#)).

According to the model for the complete set of individuals for 2nd-order selection, only 3.8% of the landscape has a good-to-high likelihood for giant anteater occurrence. This higher probability of occurrence was concentrated in the hygrophilous forest or its proximity ([Fig. 6a](#)). Adults showed a more defined pattern and model fit, so we used this age category to represent habitat selection for the 3rd order of habitat selection ([Figs. 6b–g](#)). Active anteaters used more habitats ([Fig. 6c](#)) than inactive animals, which tended to use almost exclusively hygrophilous forests ([Fig. 6d](#)). The probability of occurrence in more open habitats increased from summer to winter, but was always higher near forests ([Figs. 6e–g](#)).

DISCUSSION

Habitat selection by animals at coarser spatial and temporal scales should reveal environmental features more important to

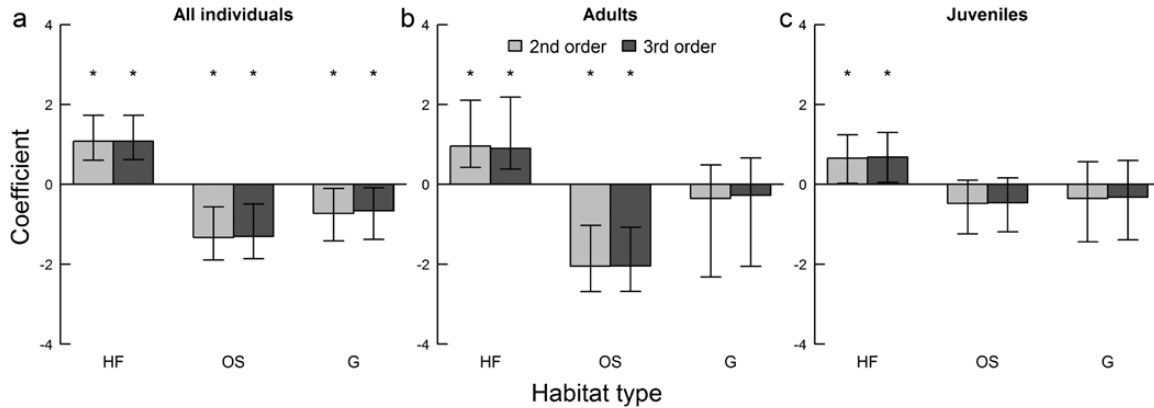


Fig. 2.—Coefficients \pm 90% CIs for different habitat types (HF = hygrophilous forest, OS = open savanna, G = grassland) according to RSF models built for different age classes: a) all individuals, b) adults, and c) juveniles. The closed savanna is used as intercept in the model. Positive coefficients indicate a positive selection. * indicates selection (90% CIs do not include zero). RSF = resource selection function.

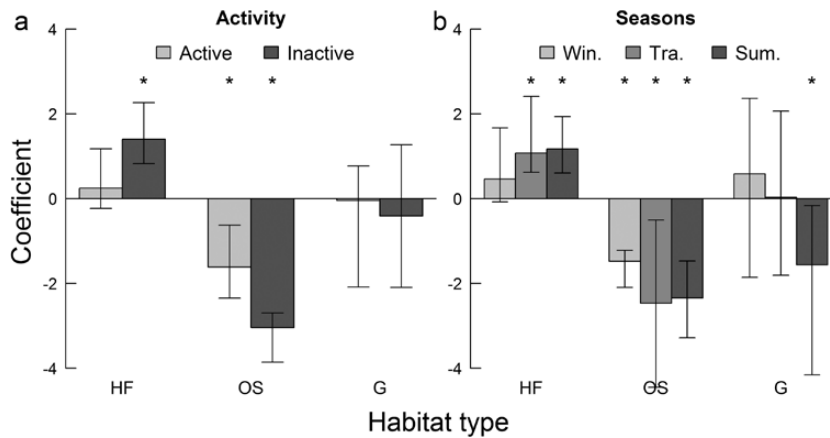


Fig. 3.—Coefficients \pm 90% CIs of different habitat types (HF = hygrophilous forest, OS = open savanna, G = grassland) selected by adults by activity a) and by season b). The closed savanna is used as intercept in the model. Positive coefficients indicate a positive selection. * indicates selection.

fitness than selection made at finer scales (Rettie and Messier 2000), but ecological patterns may be similar across some extents (Wiens 1989). Both scales examined here showed the same robust pattern, suggesting that habitat type and protection level are important predictors of habitat selection for this reintroduced giant anteater population.

The INR is a multiple use reserve, where cattle ranching is one of the main land uses. Intensive livestock grazing produce alterations on species composition and decreases structural diversity (Scimone et al. 2007; Supporting Information S1). Likewise, intentional fires for regrowth of forage and dogs (*Canis lupus familiaris*) are commonly used for cattle management. Fires and dogs, along with road kills, represent the most frequently reported direct causes of death for giant anteaters in other regions (Silveira et al. 1999; Koster 2008; Lacerda et al. 2009; Cáceres et al. 2010; Diniz and Brito 2013).

Even though anteaters could easily access PU and EI, almost all locations were confined to the strict conservation area of RS, indicating a strong avoidance of lands under livestock production. In this study, we found that habitats under livestock production at EI and PU showed diminished height and cover at the herbaceous level when compared to RS (Supporting Information S1). The ecological impacts of intensive livestock grazing

include alterations in plant and wildlife species composition and decreases in structural diversity (Jones 2002; Scimone et al. 2007), generally resulting in an extremely open vegetation structure which is probably avoided by giant anteaters. Traditional cattle ranching in INR has been associated with forest clearing, poaching, frequent fires, and the regular use of dogs, that adds further negative conditions for giant anteaters. However, it is noteworthy that EI does not use dogs and has a strict policy against hunting. Avoidance of cattle ranches could also be explained by the effect that grazing has on the ant community. However, at the study site, Calcaterra et al. (2010a) found a positive, although not significant, effect of cattle on the richness of ants in savannas, as well as a higher number of workers ants and higher ant biomass both in grassland and savannas. All these results suggest that avoidance of cattle ranches by anteaters in INR is due mainly to the effects of livestock management on vegetation structure instead of a decrease of food availability or direct mortality or harassment derived from hunting or dogs.

Roads did not affect habitat selection by giant anteaters. In the Brazilian Cerrado, anteaters selected areas removed from roads in protected areas, but they selected areas near roads in disturbed habitats (Vynne et al. 2011), suggesting that roads are not reliable predictors for habitat use by this species.

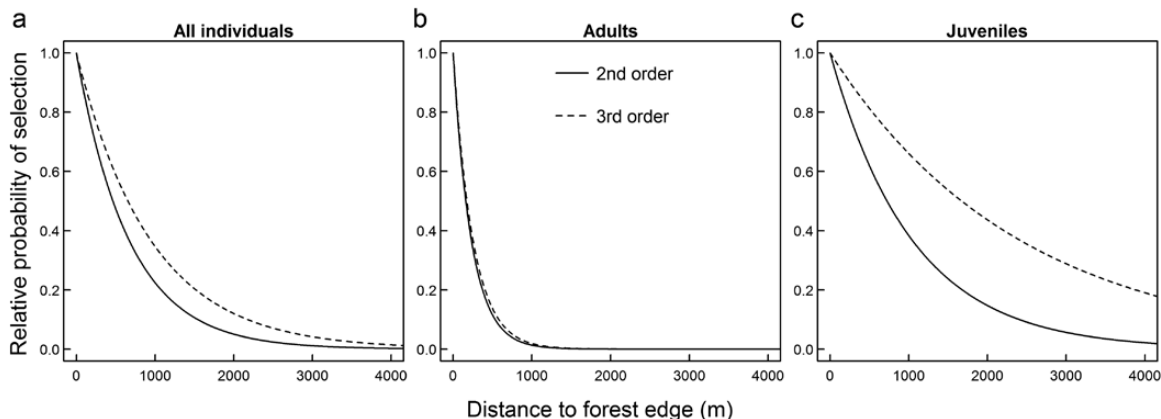


Fig. 4.—Probability of selection according to the distance to forest edge, by scale and by different age class: a) all individuals, b) adults, and c) juveniles.

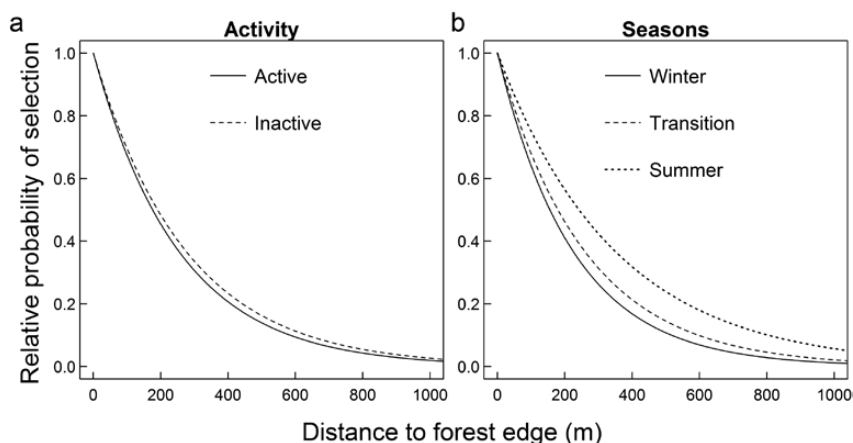


Fig. 5.—Probability of selection according to the distance to forest edge, by activity a) and by season b) for 3rd-order selection by adult individuals.

Juvenile anteaters presented a weaker pattern of habitat selection than adults. Patterns of animal movement may vary between age groups due to differences in dispersal propensity and reproductive activity (Mueller and Fagan 2008; Owen-Smith et al. 2010). Young and inexperienced animals are expected to be less efficient than adults at seeking and obtaining food (Janson and van Schaik 1993; MacKinnon 2005; Zimmer et al. 2011), probably leading to more random movements. Intraspecific competition may also explain the observed pattern of habitat selection by juveniles. Individuals forced to disperse are frequently the socially subordinate, younger, and weaker members of the population (Archer 1970; Watson and Moss 1970), with less competitive young animals being pushed into less-preferred habitats. Some degree of territoriality has been observed in giant anteaters (Shaw et al. 1987; Braga et al. 2010). At our study site, we observed 1 clear case of complete home range switch by a female after the arrival of another female that occupied the former range (Di Blanco 2015). We also observed 2 injured juvenile males whose wounds were presumably made by another anteater, suggesting that aggressive intraspecific competition and territoriality may play an important role in habitat selection patterns in giant anteaters. A long-term study of habitat use and home range dynamics as the population approaches carrying capacity could test this hypothesis.

The preference for forests by giant anteaters at our study site was also reported in wild populations of the species

(Camilo-Alves and Mourão 2006; Mourão and Medri 2007). However, a high encounter rate and a positive selection for open environments was also reported during periods of activity of wild giant anteaters (Camilo-Alves y Mourão 2006; Rodrigues et al. 2008), which was attributed to a higher abundance of food sources in them. The abundance of giant anteaters in grasslands, savannas, and dry forest biomes across the Neotropics seems to be explained by the higher food availability of these biomes when compared to humid forests (V. A. Quiroga, IBS, UNAM-CONICET, pers. comm.). Even though the savannas at our study site showed more species, individuals, biomass, and functional groups of ants than other habitat types (Calcaterra et al. 2010b), this habitat was avoided by giant anteaters even during activity periods, which suggests that food availability may not be the main factor affecting habitat selection at our study site. Positive selection of hygrophilous forests and the avoidance of open savannas at our study site may therefore be better explained by either a buffering effect of forests on extreme temperatures or from differences in perceived predation risk among environments. Currently, we do not have empirical evidence to decisively reject or support any of these hypotheses and further research should be focused at elucidating the main drivers of habitat selection on this species.

Seasonal changes in food availability may explain the seasonal shifts in habitat use by giant anteaters at our study site. Terrestrial mammals may increase movements and switch or

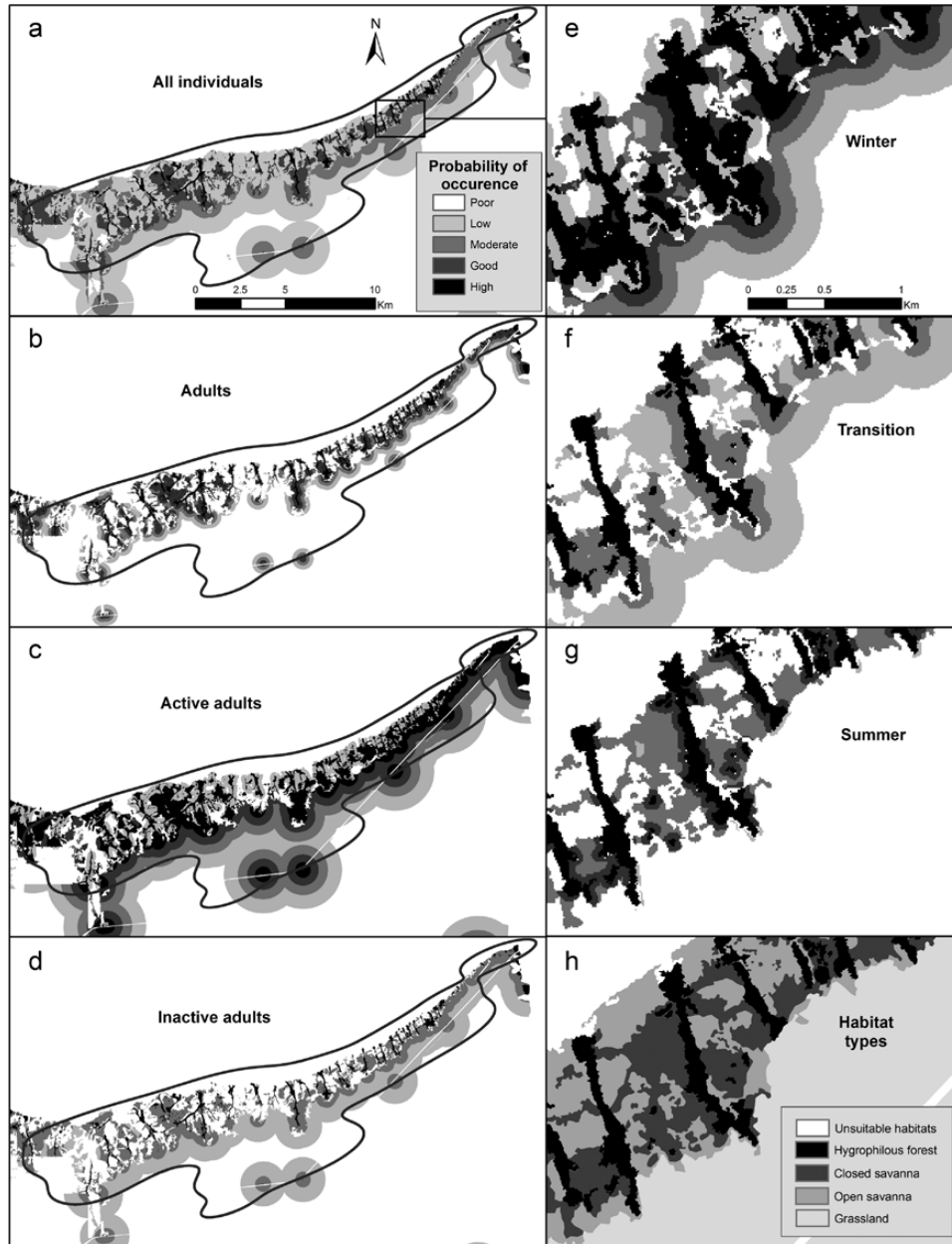


Fig. 6.—Probability of occurrence of giant anteaters according to selected covariates. a) General pattern for 2nd-order selection by the complete set of individuals. b and d) Probabilities in the entire area for 3rd-order selection from different sub-data sets. e–g) Detail of a selected area by different season. h) Habitat types as a reference.

enlarge home ranges from spring and summer to winter as local food availability declines and varies among habitats (Di Bitetti 2001; Schradin et al. 2010), which could explain the increasing use of grassland from summer to winter. The abundance of ants and termites decreases during winter in all habitats at our study site (Calcaterra et al. 2014). This reduction in food availability could have caused animals to expand their foraging areas as ants become less abundant or to visit sites perceived as risky in order to satisfy nutritional requirements (Verdolin 2006). Grasslands present areas with high abundance of ant nests of *Camponotus punctulatus*, a species that is rare in the hygrophilous forest or the savannas and that constitutes one of the most important food items in the diet of giant anteaters

at our study site (L. A. Calcaterra, FuEDEI, pers. comm.). Besides, the higher and denser grass layer found in grasslands when compared to the savannas may provide better protection against potential predators.

Species behavior can serve to identify variation in habitat quality, act as a bioindicator for the success or failure of restoration treatments (Ortega-Álvarez and Lindig-Cisneros 2012), and hence inform land management and further ecological understanding (Bennett et al. 2013). Our study may throw some light on the past, present, and future status of giant anteaters in INR and other subtropical regions. INR and the rest of Corrientes Province suffered a massive process of defaunation during the last century that resulted in the extinction of several

species, including giant anteaters. We know that the expansion of cattle production in the region during the past century was associated with the regular burning of native grasslands, the use of dogs, and deforestation (CLT 2007). Hunting was widespread in the area until probably the mid-1980s.

The effect of hunting on the survival of such a sensitive species as the giant anteater (i.e., slow moving, easy to see, and with a low reproductive rate) seems obvious. However, our results show that these animals are also sensitive to other effects derived from cattle production, expressed in decreases of forested areas and of dense and tall grass layers. Despite the remarkable variation in the habitat types used by the species, the presence of forests seems to be the key to the successful reintroduction of this species, where forest scarcity could limit the carrying capacity of this new population of giant anteaters. The avoidance of grazed habitat by giant anteaters suggests that traditional cattle ranching may not only affect the long-term abundance of the reintroduced population, but it may also indicate a potential cause for the local extinction of this and other species, such as the collared peccary, tapir, giant otter, and jaguar. Areas with forests and/or without traditional cattle management where the high grass layer can offer both food and cover seem to be a requisite for the successful reintroduction and persistence of giant anteaters and, probably, for other species that rely in vegetation cover as shelter. Hence, if giant anteaters and other species of large mammals are going to return to INR, it is important that strict conservation areas (i.e., the Provincial Park) should not be restricted to public “unproductive” marshlands but also include large representative samples of uplands habitats like the hygrophilous forests, grasslands, and savannas. In this sense, the 1,500 km² of private reserves owned by CLT covering upland habitats and placed adjacent to the marshlands protected by the Provincial Park are essential for the long-term viability or restoration of wildlife populations inside INR. Cattle ranching can also play a key role in combining biodiversity protection with traditional farming if fire, livestock carrying capacity, and dogs are managed in a way that allows for the coexistence of livestock and other large mammals.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmam-mal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Comparison of vegetation structure in lands under livestock production and strict protection in the Iberá Nature Reserve.

Supporting Information S2.—Example of the 5,000 random points generated for 2nd order of selection surface. A) Represents points totally at random and B) random points conditioned by the effect of the distance to release location, used for analysis.

Supporting Information S3.—Data sets and their corresponding competing models ranked in ascending order of AIC values.

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