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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

MOVEMENT ECOLOGY AND SPATIAL DISTRIBUTION OF *TAYASSU PECARI* IN HETEROGENEOUS TROPICAL LANDSCAPES

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ciências Biológicas (Zoologia).

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Movement ecology and spatial distribution of *Tayassu pecari* in heterogeneous tropical landscapes

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DEDICATÓRIA

Para os melhores companheiros: Fabiano e Pedro
Para meus pais Hissao e Wânia
Para meus irmãos Lígia e Victor
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SUMÁRIO

RESUMO

Modificações da cobertura do solo, perturbações antropogênicas e mudanças climáticas na região Neotropical têm sido associadas à crise da biodiversidade. Nesta tese, o objetivo principal foi investigar os efeitos que a estrutura da paisagem (incluindo a perturbação antropogênica) e a qualidade do habitat têm na distribuição espacial, nos padrões de movimento e na seleção de habitat da queixada - *Tayassu pecari*. Esta espécie é o único ungulado florestal Neotropical que forma grandes bandos e é uma espécie-chave nos ecossistemas florestais, pois sua extinção local pode causar perdas adicionais de biodiversidade por meio de efeitos em cascata. Ainda assim, pouco se sabe sobre uso do espaço e movimentos de queixadas em escala fina. Para tanto, estudamos a distribuição e movimentação da espécie em diferentes escalas e biomas do Brasil, investigando quais variáveis de paisagem influenciaram a mesma em diferentes escalas e ordens de seleção. Nossos resultados mostram fortes efeitos negativos da modificação da paisagem e fragmentação do habitat na distribuição de queixadas, restando apenas 47% do território brasileiro com áreas adequadas para a espécie. Verificamos que menos da metade de todas as áreas protegidas nos biomas Cerrado e Mata Atlântica têm um habitat adequado para a queixada. Para a análise do movimento, rastreamos 30 indivíduos com colares de GPS de julho de 2013 a outubro de 2016 no Pantanal e no Cerrado do estado do Mato Grosso do Sul. Nossos principais resultados mostraram uma seleção positiva de queixadas para áreas florestais quando comparada com a matriz composta principalmente por pastagens. Uma porcentagem maior de cobertura de árvores, maiores áreas de floresta, proximidade de fontes de água e proximidade com o centro de fragmentos tiveram um efeito positivo na seleção de habitat. A queixada evitou áreas de declividade mais íngremes, estradas pavimentadas e áreas de maior densidade populacional humana. A distância máxima que as queixadas cruzaram na matriz da paisagem não excedeu 700m. Nossos resultados mostraram que a conectividade funcional para a queixada pode ser limitada pelo tipo de cobertura da terra, por estradas pavimentadas e por regiões altamente povoadas, e essa informação pode ser aplicada para determinar novas ações de manejo de conservação em nossa região de estudo. Além disso, a distância média diária percorrida para os indivíduos monitorados foi de 3501m. O tamanho total da área de vida teve valores médios que variaram dependendo do estimador utilizado: 28 km^2 (MCP), 33 km^2 (minHREFK) e 52 km^2 (AKDE). Com este estudo, pudemos identificar que mudanças sazonais nos recursos e no contexto da paisagem podem desencadear mudanças nos padrões de movimento e na área de vida durante a vida dos animais. Analisar o comportamento de movimento e área de vida de indivíduos em diferentes biomas e escalas de tempo e espaço pode levar a diferentes conclusões sobre os requisitos de habitat para a persistência da espécie, e essa informação é essencial para a conservação da mesma em paisagens heterogêneas produtivas.

Palavras-chave: Ecologia espacial, Conservação, Ecologia de paisagens, Perda de habitat, Mamíferos, Área de vida.

ABSTRACT

Land cover modifications, anthropogenic disturbances and climate change in the Neotropical region have been linked to the biodiversity crisis. This thesis proposal was to investigate the effects that landscape structure (including anthropogenic disturbance) and habitat quality have in the spatial distribution, in the movement patterns and in the habitat selection of the white-lipped peccary - *Tayassu pecari* (WLP). This species is the only Neotropical forest ungulate that forms large herds, and it is a keystone species in forest ecosystems because its local extinction may cause additional biodiversity losses through cascading effects. Still, little is known about WLPs space use and fine-scale movement. For that aim we studied the species distribution and movements in different scales and biomes of Brazil, investigating which landscape variables would influence the species in different scales and orders of selection. Our findings show strong negative effects of landscape modification and habitat fragmentation on white-lipped peccary distribution, with only 47% of the Brazilian territory with suitable areas for the species. We also found that less than half of all protected areas in the Cerrado and the Atlantic Forest biomes have suitable habitat for WLP. For the movement analysis we tracked 30 individuals with GPS collars from July 2013 to October of 2016 in the Pantanal and in the Cerrado of Mato Grosso do Sul state. Our main results showed a positive selection of WLP for forest areas when compared with the matrix composed mainly by pasture. A higher percent of tree cover, larger forest patches, proximity to water sources and proximity with fragment center had a positive effect on habitat selection. WLP avoided steep slope areas, paved roads, and areas of higher human population density. The maximum matrix crossing distance for pasture cover did not exceed 700m. Our results showed that functional connectivity for WLP can be limited by land cover, roads and highly populated regions and this information can be applied to determine new conservation management actions in our study region. Also, the mean daily distance traveled for the monitored individuals was 3501m. The total home range size had mean values varying depending on the estimator used: 28 km^2 (MCP), 33 km^2 (minHREFK) and 52 km^2 (AKDE). With this study, we could identify that seasonal changes in resources and the landscape context can trigger changes in the movement patterns and in the home range during the animals’ lifetime. Analyzing movement and home range behavior of individuals in different biomes and scales of time and space can drive different conclusions about the habitat requirements for the species persistence, and that information is essential for its conservation in heterogeneous productive landscapes.

Keywords: Spatial Ecology, Conservation, Landscape Ecology, Habitat loss, Mammals, Home range.

I INTRODUCTION

Land-use changes have been causing reduction of terrestrial biodiversity globally (Newbold et al., 2015). Anthropogenic impacts associated with landscape alterations can direct or indirectly affect biodiversity, and one of the main current impacts is habitat loss and fragmentation. These land-use m theodifications can affect the range (Yackulic et al., 2011), movement (Tucker et al., 2018), and activity patterns (Gaynor et al., 2018) of mammal population. Therefore, currently a central challenge for the conservation biology of mammals is to monitor the influences and predict the future consequences that environmental changes have on animal populations' distribution and persistence.

In heterogeneous environments, investigating how the landscape structure (composition and configuration) affects range distribution, home range and movements of animals allow us to understand what the habitat requirements for species persistence are. We can also gain insights on how individuals are currently adapting their movements (inside and among habitat patches), space use and activity patterns to survive in altered landscapes (Fahrig, 2007; Gaynor et al., 2018; Shepard et al., 2008). Understanding and simulating how landscape changes will affect natural populations and communities in the long-term are important steps for determining more effective conservation actions' planning (e.g. Crouzeilles et al., 2015; Hanski and Gilpin, 1991; Jeltsch et al., 2013; Morales et al., 2005).

Exploring the effects of habitat loss and fragmentation in habitat selection may also require multi-scale approaches (Benhamou, 2014; Mayor et al., 2009; McGarigal et al., 2016) to explore how the impacts of landscape alterations can change if we focus in a different scale of analysis. Habitat selection assumes a disproportional use of space when comparing used versus available habitat categories (Beyer et al., 2010; Johnson, 1980; Lele et al., 2013). Multi-scale approaches explore how different spatial scales can affect the ratios of use and availability in habitat selection (Mayor et al., 2009). In addition, habitat selection may not be scaled up or down because different habitat variables can be selected in different scales and consequently the tradeoff between fitness costs and benefits can also be affected differently depending on the scale of analysis (Mayor et al., 2009; McGarigal et al., 2016). Thus, using a multi-scale approach allows to evaluate and to quantify those differences.

Another challenge to integrate landscape elements in habitat selection studies is evaluating the hierarchical nature within different orders of selection (Johnson, 1980; McGarigal et al., 2016). This evaluation comprise exploring the selection in the range distribution of a species (first order), the home range of individuals (second order), the habitat components within the home range (third order), and finally, the specific habitat components in focal sites for feeding or specific resources in preferred core areas of use (fourth order) (Johnson, 1980). More than a multi-scale approach, knowing the different impacts that landscape structure can have for species persistence in those different orders of selection, require thinking also about which biological responses and ecological processes are affected in each scale. Information provided for those different orders of selection can help to develop conservation strategies in different economic and political levels (i.e., local, regional and global).

Using multi-scale approaches to define what are the main scales in which different species respond (and how that response happens) to land-cover change, fragmentation, agriculture expansion, and creation of barriers such as roads is of extreme importance to determine how the anthropogenic matrix affects the permeability for different species, and how functional connectivity can be re-created in a dynamic changing world (Fahrig, 2017; Vasudev and Fletcher, 2015). However, it is also necessary to avoid confounding effects that fragmentation per se can have on different biological groups to determine the positive and the negative effects of landscape modifications on biodiversity (Ewers and Didham, 2006; Fahrig, 2017, 2003).

Spatial data collected using GPS technology can provide new information about behavior and decisions made by animals while moving through the landscape (Fortin et al., 2005; Gurarie et al., 2016). This information combined with new statistical approaches create new possibilities to explore species spatial distribution, movement behavior and habitat selection changes with much more detail and in shorter periods of time (Bracis et al., 2018; Gurarie et al., 2009; Morales et al., 2004; Ovaskainen et al., 2014). It also makes the identification of ecological corridors and key habitats a more dynamic and reasonable task (Chetkiewicz et al., 2006; Thurfjell et al., 2014; Vasudev and Fletcher, 2015). This is especially interesting for forest mammals that are sensible to habitat loss and fragmentation (Magioli et al., 2015; Pardini et al., 2017) since habitat alteration and anthropogenic impacts also affect mammal occurrence, movements and space use patterns (e.g. Beca et al., 2017; Betts et al., 2017; Davies et al., 2017; Ferreira et al., 2017; Morato et al., 2016; Tucker et al., 2018). Therefore, the use of environmental thresholds to predict effects of habitat loss on biodiversity occurrence and movement, may produce valuable information for species conservation, especially for forest dependent mammals.

Usually, monitoring the movement of several species in a given area is difficult and expensive. Surrogate species may be used to understand the effects of landscape composition on biodiversity by monitoring a few key species, due to the high costs to study and to create strategies to protect all threatened species (Sanderson et al., 2002). Because of their biological requirements and ecological role in forest ecosystems, the white-lipped peccary (WLP) (*Tayassu pecari*) is a good example of a surrogate species to identify the effects of habitat loss and modification on forest dependent mammals (Altrichter et al., 2012; Jorge et al., 2013; Keuroghlian et al., 2015; Reyna-Hurtado et al., 2016). They are frugivorous-omnivorous ungulates living in large herds and composing the largest biomass of mammals in the Neotropical forests (Beck, 2006; Eisenberg, 1980; Peres, 1996). WLP depend on forests to survive, and the forests are also affected by their absence because the extirpation of WLP may cause habitat alterations and additional biodiversity losses (Altrichter et al., 2012; Beck, 2006; Galetti et al., 2017; Keuroghlian et al., 2015; Keuroghlian and Eaton, 2009, 2008a). For all those reasons, WLP is excellent candidate to be used as surrogate "*landscape species*" (Sanderson et al., 2002) allowing deeper understanding of how landscape structure and anthropogenic impacts can affect the distribution and movements of other medium and large sized forest mammals.

Finally, despite the progress on the habitat selection and movement ecology research, much work is needed to account for the types of movement behavior often observed in long-lived species with spatial memory, learned behavior and social structure (Fryxell et al., 2008; Morales et al., 2004; Mueller and Fagan, 2008). Therefore, the study of the WLP habitat selection and movement addresses new information for movement ecology itself and may provide answers about what are the habitat-specific parameters and traits of large social mammals that influence their population persistence in altered landscapes.

1.1. General objectives

Our main objective in this research was to understand the effects that landscape structure (including anthropogenic disturbance and habitat quality) have in the habitat suitability and in the fine-scale movement patterns of WLP. Thus, we studied the species distribution and movements in different scales and biomes of Brazil, investigating which landscape variables would influence the species in different scales and orders of selection. More specifically, in this research we ask:

In Chapter 1 - *Bioclimatic and landscape suitability models as planning tools for the conservation of a Neotropical forest ecosystem engineer*

1. What is the amount of remaining suitable habitat areas for WLPs in Brazil?
2. Is habitat suitability in different regions of Brazil predicted by the same landscape and bioclimatic variables?
3. How are the remaining suitable areas distributed across different Brazilian biomes?
4. How forest loss in recent years affected the amount of suitable habitat available for the WLPs in Brazil?

In Chapter 2 - *Planning my next step: how landscape variables influence movement decisions of a forest ungulate within tropical landscapes?*

1. What are the main landscape variables that influence movement decisions and habitat selection for WLPs in the Pantanal and Cerrado of Mato Grosso do Sul state?
2. What is the gap crossing capacity for the species in the studied region?

In Chapter 3 - *Can movement patterns, home range and displacement rates be used as indicators of habitat quality for the last large-herd-living ungulate of neotropical forests?*

1. Do WLP herds in the Pantanal and Cerrado display similar patterns of movement, home range and displacement?
2. Is there a difference in the movement patterns of male and female WLPs?
3. Can we detect different movement modes and average daily distance traveled per day in the different seasons and regions of study?
4. How landscape structure is influencing the herds' space use patterns and can we detect non-optimal movements of WLP in response to landscape modification and habitat disturbance?

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II CHAPTER 1

Bioclimatic and landscape suitability models as planning tools for the conservation of a Neotropical forest ecosystem engineer

ABSTRACT

Land cover modification, anthropogenic disturbance and climate change in the Neotropical region have been linked to the biodiversity crisis. Herein, we applied coupled habitat suitability models to investigate the effects of climate, landscape and anthropogenic variables on the distribution of a Neotropical forest ecosystem engineer, the white-lipped peccary (WLP). We also evaluated the effects of forest loss on its local persistence. Our findings show strong negative effects of landscape modification and habitat fragmentation on white-lipped peccary distribution, with only 47% of the country having suitable areas for the species. Less than half of all protected areas in the Cerrado and the Atlantic Forest biomes have suitable habitat for WLP. We define regions that could guide different conservation management strategies and we suggest that conservation actions are essential to slow down and possibly reverse current population trends and declining geographic distribution, thereby averting a possible collapse of forest ecosystem functioning in the Neotropical region in the future. Improved understanding of the habitat suitability of this species can also help predict how impacts of habitat loss will affect other medium and large-sized forest mammals.

Keywords: *Tayassu pecari*, species distribution model, fragmentation, habitat loss, defaunation, ecosystem functionality

1. INTRODUCTION

Climate change and landscape modification are listed as major causes of biodiversity loss worldwide (Barlow et al., 2016; McGuire et al., 2016; Newbold et al., 2015, Estrada et al. 2016). However, species responses to climate change, land cover alterations, habitat loss and fragmentation, and other human impacts (such as hunting, creation of artificial barriers and pollution) are still unclear (Behr et al., 2017; Beyer et al., 2010; Newbold, 2018; Ovaskainen et al., 2014; Struve et al., 2010). Habitat Suitability Models have been used to assess the effects of climate change and landscape modification on biodiversity (Elith and Leathwick, 2009) and predict future consequences of environmental changes on biodiversity at narrow to broad scales (Crouzeilles et al., 2015; Hanski and Gilpin, 1991; Newbold, 2018) to define goals and regions where conservation management actions can be applied and could be most effective.

Investigations linking use of space to habitat selection have been central areas of ecology since the first definitions of niche theory (e.g. Elton, 1927; Grinnell, 1917; Hutchinson, 1957; Peterson et al., 2011). This is still the aim of recent attempts to create new statistical tools, sampling and modeling protocols (Behr et al., 2017; Fortin et al., 2005; Merow et al., 2016; Moorcroft et al., 2006; Morales et al., 2004) that can more accurately depict the causes and effects of habitat selection (Beyer et al., 2010) in determining species persistence in disturbed areas (Morrison et al., 2007; Shackelford et al., 2018).

Mammals play key roles in forest ecosystems (Schipper et al., 2008), but defaunation induced by hunting pressure (Antunes et al., 2016), fragmentation and habitat loss (Fahrig, 2003; Pardini et al., 2017) have been so drastic that they can be considered new drivers of a mass extinction event (Barnosky et al., 2011; Galetti et al., 2017). Currently, over 27% of all mammal species are threatened (Schipper et al., 2008), which makes selecting surrogate species and biodiversity hotspots to optimize conservation targets both urgent and necessary (Ceballos and Ehrlich, 2006).

White-lipped peccaries (WLP) are the only Neotropical forest ungulates that form large herds (Sowls, 1984) and, therefore, they exert strong local top-down effects on forest ecosystems (Keuroghlian et al., 2009). Regionally, their extirpation from forest areas may cause additional biodiversity losses through cascading effects (Altrichter and Almeida, 2002; Keuroghlian et al., 2009; Keuroghlian and Eaton, 2008b), which makes them key species for the conservation of Neotropical forests. Due to the impacts of WLP herds on soil, litter, plant recruitment, and dispersal, the species directly and indirectly alters its environment, with associated effects on other animals and plants (Keuroghlian and Eaton, 2009). Thus, they also function as ecosystem engineers (Beck et al., 2010; Ringler et al., 2015).

Due to habitat loss and hunting (Antunes et al., 2016; Keuroghlian et al., 2017; Peres, 1996), WLPs have shown reduced abundance and low probability of long-term survival within 48% of their current distribution range (Altrichter et al., 2012), thereby being classified as Vulnerable on the IUCN Red List. Additionally, WLPs experience other impacts caused by direct contact with livestock, including infectious diseases (Freitas et al., 2010; Fragoso, 2004). Recent studies indicate that a reduction in WLP abundance and geographic distribution will continue for the next three generations (Keuroghlian et al., 2013).

Selective habitat use associated with extensive home ranges and movements (Altrichter and Almeida, 2002; Carrillo et al., 2002; Fragoso, 1998; Hofman et al., 2016; Jorge et al., 2019; Keuroghlian et al., 2015; Reyna-Hurtado et al., 2012) renders WLPs an ideal species to investigate how landscape alterations influence their spatial distribution, with similar consequences for other large-bodied neotropical forest mammals. For this purpose, we quantified the amount of remaining suitable habitat areas for WLPs in Brazil, the country with the largest portion of the species current range (68.4% or 7,336,197 km^2) (Altrichter et al., 2012). Once the primary criteria that influence the presence of WLP populations within different biomes are established, areas for conservation actions that will benefit regional biodiversity can be prioritized. Furthermore, we asked if WLP habitat suitability in different regions of Brazil can be predicted by landscape and bioclimatic variables, and how the remaining suitable areas are distributed across different Brazilian biomes. Finally, we discuss how forest loss in Brazil in recent years affects the amount of suitable habitat available for the species.

2. MATERIAL AND METHODS

2.1. Model species

The White-lipped peccary (*Tayassu pecari*) (Link, 1795) is one of three species belonging to the Tayassuidae family, in the superorder Cetartiodactyla. This social, frugivorous–omnivorous ungulate is distributed across the Americas (Figure 1) from southeastern Mexico to northern Argentina and southern Brazil (Beck et al., 2017; Sowls, 1997). The species presents some plasticity in occupying different vegetation habitats (*e.g.*, rainforests, dry forests, savannahs, and wetlands), but preferentially uses forest habitats and riparian zones (Fragoso, 1999; Keuroghlian et al., 2013; Keuroghlian and Eaton, 2008b). WLP is also the only large-herd-living neotropical forest ungulate, being a highly social species with a promiscuous mating system (Leite et al., 2018) that often forms herds larger than 100 individuals, of both sexes and different age classes (Biondo et al., 2011). In Brazil the species is considered Vulnerable by the IUCN, and it is almost locally extinct in the Caatinga biome, where the species have faced population reduction of more than 30% in the last decade (Keuroghlian et al., 2012). In this arid biome the species is mainly threatened by habitat modification, deforestation and hunting, and it only occurs in specific protected areas of the Parque Nacional do Boqueirão da Onça, Parque Nacional da Serra da Capivara, Parque Nacional da Serra das Confusões and in the region where the creation of a new protected area is being proposed, the Parque Nacional da Serra Vermelha.

With adults weighing 30 kg on average (Keuroghlian and Desbiez, 2010), WLP represent the largest mammal biomass in the Neotropical forests where they are present (e.g. Beck, 2006; Eisenberg, 1980; Peres, 1996). WLP have important ecological roles: as prey for large carnivores (e.g. the jaguar, *Panthera onca*, and the cougar, *Puma concolor*), as seed predators and dispersers, and as ecosystem engineers due to their impacts on forest structure during foraging and resting, since they create new environments through soil and plant trampling (Keuroghlian and Eaton, 2008a; Kiltie and Terborgh, 1983; Ringler et al., 2015). WLP herds can have daily movements of 3.8 km (Hofman et al., 2016) to 10 km (Kiltie and Terborgh, 1983) and their fusion-fission social structure is characterized by the formation of herds that are divided into sub-herds, with frequent exchange of individuals (Keuroghlian et al., 2004). Home range size of a single herd can vary from 15 to 200 km^2 (Bodmer, 1990; Carrillo et al., 2002; Fragoso, 1998; Keuroghlian et al., 2004,2015; Kiltie and Terborgh, 1983; Reyna-Hurtado et al., 2009).

2.2. Presence records

A database with geographic locations and presence records of WLPs in Brazil was constructed based on a literature review and specialized databanks (Figure 1). Only primary records (direct observations, camera trap data, footprints and hair) collected between 1987 and 2017 were considered. The revision was mainly based on the data bank provided by Altrichter et al. (2012) and Jorge et al. (2013), a database from the Chico Mendes Institute for Conservation (ICMbio, a Brazilian environmental agency) and field observations collected by specialists, scientific articles and reports including the conservation management plan for protected areas and conservation action plan for WLPs (Keuroghlian et al., 2012). Most information from museums and other databases such as the Global Biodiversity Information Facility (GBIF, 2012) were already registered in the other databanks or were registered prior to 1987, so we opted not to use them. We georeferenced some occurrence records *a posteriori* if the information source mentioned farm or reserve names and included survey positions (camera trap, sighting or transect positions). In cases where the exact position was not clearly reported, we opted to use centroid positional estimates within a known forest fragment or protected area that had been explicitly mentioned in the original reports.

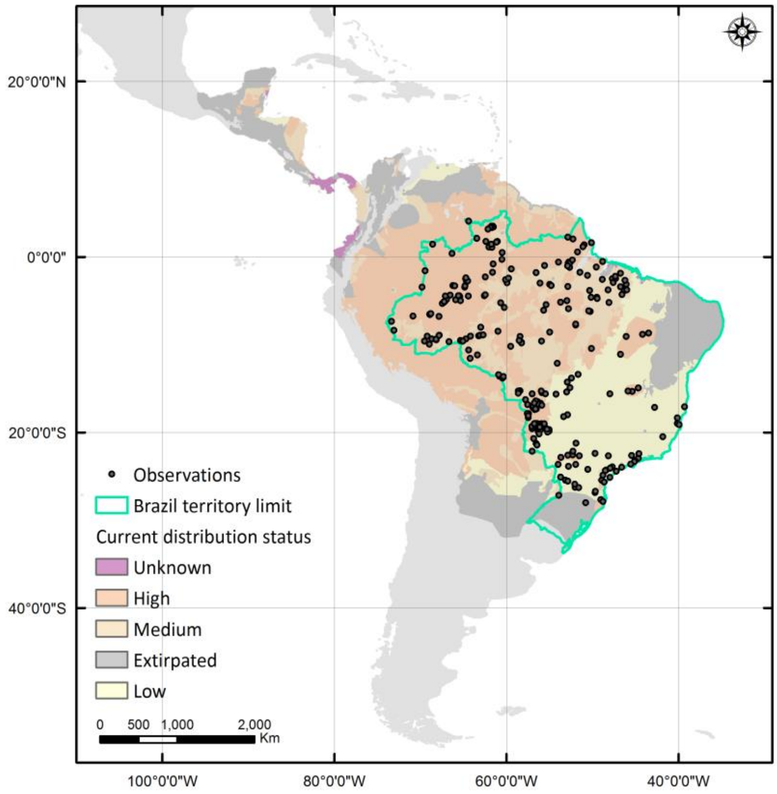

Figure 1. Primary records of white-lipped peccaries *Tayassu pecari* in Brazil recorded between 1987 and 2017. Different colors show the current distribution status of the species per region according to Altrichter et al. (2012).

2.3. Environmental predictors

Four environmental layer categories were used to model habitat suitability for WLP: a) bioclimatic, b) topographic, c) landscape and d) anthropogenic.

2.3.1. Bioclimatic

Bioclimatic variables were gathered from the open global climate database CHELSA (Karger et al., 2017). Among the 19 available bioclimatic variables, we used a factorial analysis and Pearson's correlation coefficient to identify highly correlated variables (correlation coefficient > 0.7) and removed those from the suitability modeling. Our factorial analysis identified four fairly independent bioclimatic variables, chosen for white-lipped peccary climatic modeling: Isothermality (BIO3) – which consists of (Mean Diurnal Range - BIO2 / Temperature Annual Range - BIO7) (* 100), Mean Temperature of Warmest Quarter (BIO10), Precipitation of Wettest Quarter (BIO16), and Precipitation of Driest Quarter (BIO17).

2.3.2. Landscape

Percentage of tree canopy cover was obtained from the Global Forest Change databank (Hansen et al., 2013) for the entire Brazilian territory. We also used this classification to build a layer of patch size, with percentage of tree canopy cover data >= 25%, considered here as the total connected forest patch size (side by side pixel and diagonal pixels connected) for each individual forest patch. Distance from forest patch edge was also calculated based on the previous patch classification. We used the edges as a zero line, therefore distance measured in meters had positive values in the matrix and negative when inside the forest patch, both with increasing values as distance increased from the border/edge line. The size of the fragment patches and the distances from patch edges were calculated using the GRASS GIS (Neteler et al., 2012) extension for landscape metrics calculation from the Spatial Ecology and Conservation Laboratory (LEEC) - LSMetrics (https://github.com/LEEClab/LS_METRICS, Niebuhr et al. in prep.).

Spatial heterogeneity (i.e. habitat diversity) was based on the Global Habitat Heterogeneity database (Tuanmu and Jetz, 2015) which has metrics based on enhanced vegetation index (EVI) imagery from Moderate Resolution Imaging Spectroradiometer (MODIS). The metric used was homogeneity, a second-order texture metric based on the similarity of EVI between adjacent pixels, and negatively correlated with heterogeneity. The data was obtained from EarthEnv (https://www.earthenv.org/texture).

We also used a layer of an inland surface water frequency dataset (GIW) (Feng et al., 2016). The GIW is publicly available at the GLCF website (http://www.landcover.org) and it is based on a global, high-resolution (30-m) inland water body dataset from 2000. This layer was used to test the effects of seasonally inundated areas on suitable areas for the white-lipped peccaries, especially in the Brazilian Pantanal and Amazon, where the effects of seasonal flooding are important for shaping those dynamic landscapes.

2.3.3. Topographic

Terrain slope information was acquired from an SRTM derivative data from TOPODATA databank, a Brazilian Geomorphometric Database (de Morisson Valeriano and de Fátima Rossetti, 2012; Valeriano, 2008) available on the Ambdata website (http://www.dpi.inpe.br/Ambdata) from the Brazilian Institute of Space Research (INPE).

2.3.4. Anthropogenic

We used two anthropogenic layers as proxies for human disturbance and accessibility: human density and density of paved roads. Human density layer was based on the human population density information provided by the 2010 census from the Brazilian Institute of Geography and Statistics (IBGE, www.ibge.gov.br). We downloaded the entire vector data containing the census results that are available in the IBGE FTP server (ftp://geoftp.ibge.gov.br/recortes_para_fins_estatisticos/grade_estatistica/censo_2010/). The data was rasterized and we created a final raster mosaic for the Brazilian territory with the number of humans per km^2. Density of paved road was based on the shapefile of existing roads, which is freely available from the Departamento Nacional de Infra-estrutura de Transportes (DNIT, http://servicos.dnit.gov.br/vgeo/). Using the DNIT classification we selected only the existent paved roads and calculated the kernel density for these roads for all the Brazilian territory, we tested this variable as an access bias prior rather than a covariate, which is explained in the next sections.

All predictors were rescaled and/or calculated with a resolution of approximately 1 km^2 (0.00833º) and projected to WGS 84 geographic system using ArcGIS 10.2. We then looked for collinearity among all layers using bivariate Pearson correlations (Supplementary material). Percentage of tree canopy cover and patch size were correlated, which is why we only chose percentage of tree canopy cover for the models, and we used patch size to classify the suitable fragments and distinguish between fragments that we consider functional or non-functional. This is explained in the *Final modelling approaches* section of the Methods. All other covariates had correlation coefficients smaller than 0.7, indicating that multicollinearity was not high.

2.4. Spatial and environmental rarefaction of occurrence data

As the 318 records of white-lipped peccaries from the Brazilian territory were based on literature review and on sighting records of specialists collected during fieldwork, we applied a filter to avoid autocorrelation caused by sampling bias, which can significantly affect the models' predictions (Fourcade et al., 2014; Merow et al., 2013; Redding et al., 2017). We used the SDMtoolbox (Brown, 2014) in ArcGIS 10.2 to filter occurrence data that could possibly have similar environmental information or were spatially clumped, as well as to remove possible duplicated data. We applied a minimum distance radius of 5 km and a maximum of 50 km to filter data with an environmental rarefaction based on distance and using a 5 class heterogeneity layer. We used these distances because we consider that data representing similar environmental information would lie within those distance radius. The five classes of heterogeneity were generated using the percent of eigenvalues from the principal component analysis (PCA) of all the environmental predictors' standardized values. We used the natural breaks classification to define the breakpoints for the five classes of heterogeneity and maximize the differences between the classes. After the rarefaction procedure, we retained 278 occurrence records for the suitability models.

2.5. Sampling bias correction of occurrence data

Biased sampling patterns can emerge from different datasets because of access facilities used by researchers, such as distance from roads, rivers or forest edges. In habitat suitability models, identifying and removing sampling bias from occurrence data is important because of assumptions of normality in the distribution of the data that are used to develop the model (Elith et al., 2011). If the occurrence data has a sampling bias, final estimates will also be biased, especially if the model has predictors that are proxies for anthropogenic variables and that correlate with the access routes such as rivers and roads. Indeed, Oliveira et al. (2016) showed that the Brazilian biodiversity data (all taxonomic groups, including vertebrates) is spatially correlated with access routes by roads and rivers (this last one more specifically related to the Amazon).

Accounting for biased occurrence data in the model can be done using a bias file within the MaxEnt algorithm in two ways (Merow et al., 2013). The first one is to change the way the prior information about the species distribution is given in the model. We substituted the generally used spatially uniform prior with a biased prior that accounted for variation in the occurrence data. The second alternative is to delimitate a boundary for the sampling of background points, so that the uniform prior is maintained but the selection of background points is limited spatially, similar to the distribution of occurrence points (Fourcade et al., 2014; Merow et al., 2013).

We opted for testing for bias correction using two types of bias priors: (1) using an access bias prior that was composed of the density raster of access routes (kernel density of paved roads and main rivers in the Amazon biome) and (2) a bias' prior that was created using a kernel density function with all WLP occurrence points. We analyzed and compared the area under the operator curve values and also the corrected Akaike Information criteria (AICc) with the MuMIn (Bartoń, 2016) package values between the MaxEnt models (without and with the two bias corrections), using the linear feature (LF) and default sets with all possible features – hinge, product, linear, threshold and quadratic (allF).

We also used this same procedure for models with and without forest edge distance as predictor since we hypothesized that edge distance was another important environmental variable to explain WLP distribution. We realized that this could also be causing overfitting in the model due to sampling bias efforts, so we wanted to check how much improvement that predictor would bring to the model. Comparisons were carried out following the methods proposed by (Fitzpatrick et al., 2013) to check if the bias correction caused by accessibility could improve predictions within the MaxEnt models with and without the forest edge distance predictor. Results are presented in the supplementary material as there was no improvement in predictions with bias corrections and final models were created without bias correction and without the forest edge distance variable included.

2.6. Final modelling approaches

Four algorithms based on presence-only data were tested to analyze habitat suitability for WLP using the packages dismo (Hijmans et al., 2017) and kernlab (Karatzoglou and Feinerer, 2010). The four algorithms chosen were: (1) Bioclim (Nix, 1986), mostly used as 'climate-envelope-model', this algorithm is based on values of similarity between environmental values of a given location with values associated with known presence record locations used for train. Suitability is higher when values are closer to the 50th percentile (median) (Hijmans et al., 2017); (2) Domain—Gower distance (Carpenter et al., 1993), where similarity between environmental variables is based on the Gower distance, a similarity coefficient, between any location (where one wants to estimate suitability) and a known presence record location (Hijmans et al., 2017); (3) Support Vector Machines (SVM) (Tax and Duin, 2004); machine learning algorithm which apply linear methods to the data in a high-dimensional feature space to identify patterns associated with the species presence records and (4) Maximum Entropy (Elith et al., 2011; Phillips et al., 2004; Phillips et al. 2017), MaxEnt (v 3.3.3k), which is the most widely-used software, and a machine-learning algorithm based on maximum entropy principles (Merow et al., 2013).

We fitted all models using a partitioning criterion to randomly select 75% of data for training and 25% for the test, with 10 replications per algorithm and four algorithms (Bioclim, Gower distance, SVM and MaxEnt). To measure accuracy in the predictions, we used the area under the receiver operating curve (AUC), and we considered that models with AUC > 0.7 were good for uncovering distribution of suitable areas for WLP, while models with AUC < 0.7 and > 0.5 were fair. We used MaxEnt default set in R with the dismo package (Hijmans et al., 2017), and the logistic outputs for the suitability models, but we set jackknife of regularized training gain to true to calculate the predictors' percent of contribution, and set 10,000 background points and 500 iterations for the runs.

For each model we used the *maximum training sensitivity and specificity* as the threshold to obtain binary raster maps of suitability (Liu et al., 2013), where each cell had values of 0 (unsuitable) or 1 (suitable). We then summed the 40 output raster maps (10 runs for each of the four algorithms) and obtained a map with values ranging from 0 to 40, representing the frequency that each raster cell was predicted as suitable. We divided the cell values by 40 to set the values to a scale of 0 to 1. We used 0.25 as the lowest presence threshold (LPT), which is the lowest suitability value associated with the species presence record, to standardize the threshold for model cut-off for the different models, and compute the final predicted binary map with all the algorithm maps (Pearson et al., 2007).

We used ensemble forecasts (Araujo and New, 2007) to make a unique raster composed of the frequency of suitability values for the 40 models. We first modelled the habitat suitability for WLP using all the predictors together in a so called standard model, which was the base model to determine suitable areas for the species and for further analysis of forest cover loss impacts. For this model, we calculated the frequency in which each cell was predicted as suitable, as well as the mean and standard deviation of the 40 models. In a second analysis, we modeled the climatic suitability for WLP using only the bioclimatic variables as predictors (BIOS 3, 10, 16, 17) and landscape suitability using only the landscape, topographic and anthropogenic variables (percent of tree cover, homogeneity, inland water frequency, terrain slope and human density).

The importance of each variable to determine habitat suitability for WLPs was tested by overlapping the 278 occurrence records with the 9 environmental variables and we extracted the value of each variable pixel in the presence records positions. After standardizing the values we performed a principal component analysis (PCA) to explore how the magnitude of values varied between the four Brazilian biomes where the species occurs (Atlantic Forest, Cerrado, Pantanal and the Amazon), which represents the environmental space used by the species in Brazil (Janekovi and Novak, 2012; Moreira et al., 2014). We also assessed the Jacknife training gain results for the MaxEnt models of habitat suitability for WLPs.

2.7. Summed model

In a second approach, named as the *Ecoland modelling* (Sobral Souza et al., in prep.), we used separated environmental categories for modeling, which consist of comparing and using the two different result models (e.g. Climatic and Landscape) summing them to compose a new map for classifying regions based on the combination (interaction) of climatic and landscape suitabilities (Figure 2). It is possible to identify areas where conditions from both models are highly suitable for WLP, areas where conditions from both models are highly unsuitable, and areas where conditions from each model are discrepant, with high climatic suitability and low landscape suitability, or vice-versa. The Ecoland approach used our final modelling to provide better tools for the species conservation (See Discussion).

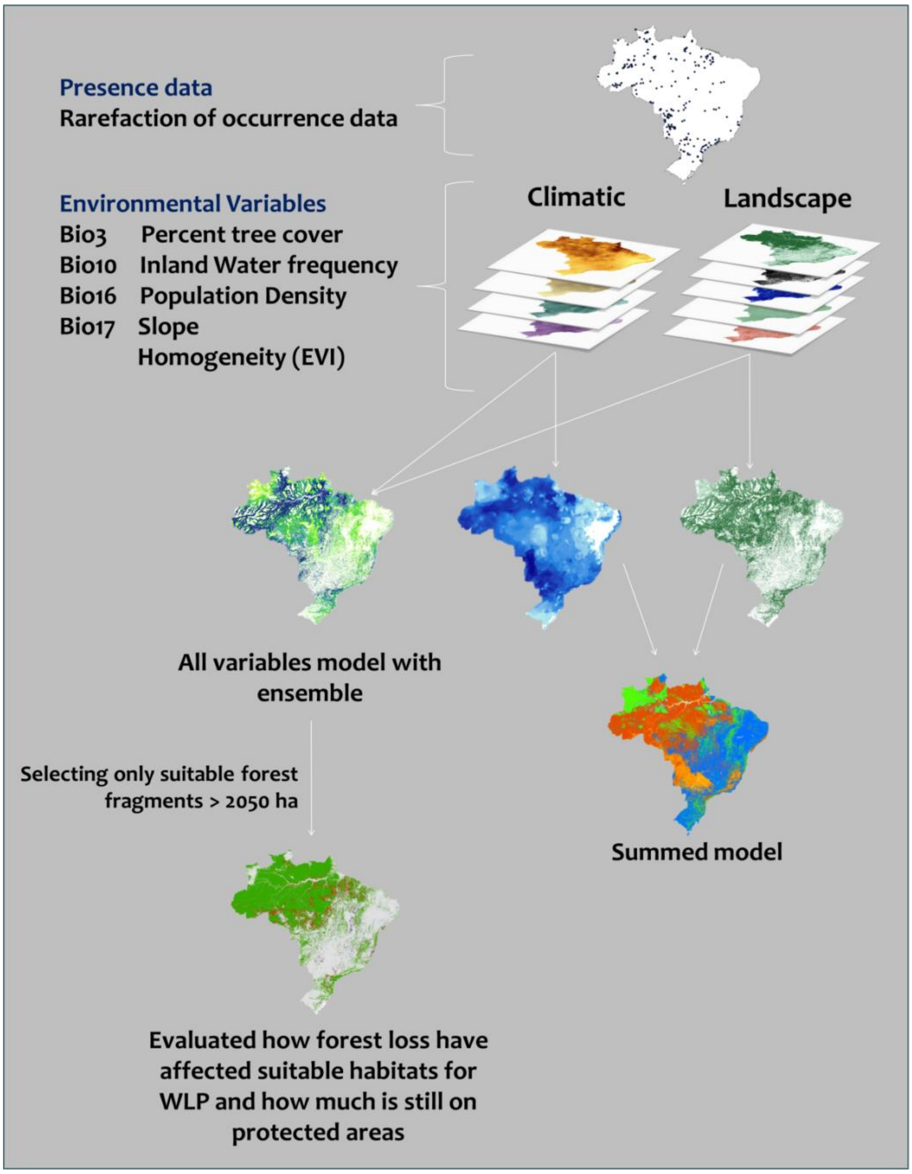

Figure 2. A conceptual framework to explain the final modelling approach and all the variables tested.

2.8. Suitable functional forest fragments evaluation

We used the results from the standard ensemble model with a resolution of 1 km^2, projected to South America Albers Equal Area Conic projection system and filtered by the LPT threshold value of 0.25 (Pearson et al., 2007) as suitable for the species. We then evaluated how much of the suitable areas were too small to retain viable populations of WLP, based on the size of the forest patches where we verified the presence records that were revised for this study and using information about home range size described in the literature (Fragoso, 1998; Jácomo et al., 2013; Keuroghlian et al., 2004). We established a threshold of

2050 ha (20.5 km^2), which was shown to be an important threshold area for sensitive species such as WLPs in a study about functional diversity of Neotropical forests (Magioli et al., 2015), and used the patch size raster to identify forest fragments that were larger than 2050 ha. Individual forest fragments larger than 2050 ha were numerically classified (by patch individual identification) so that we could more precisely calculate the area that is still functionally suitable for the species. Next, we were able to calculate how much forest cover loss affected suitable areas between 2000 and 2016. After this calculation, we identified the percentage of forest area loss, using data of total area of gross forest cover loss available from the Global Forest Change databank (Hansen et al., 2013) with the resolution rescaled to 1 km^2. We did this for each one of the biomes (Amazon, Cerrado, Atlantic Forest and Pantanal), using the delimitation provided by IBGE 2016, to make a new evaluation of the suitable areas not affected by loss during this period.

The last analysis quantified how much of these areas were inside protected areas using the shapefile of the Brazilian Environment Ministry (available at http://mapas.mma.gov.br/i3geo/datadownload.htm) as a mask to calculate how many of suitable functional areas are effectively within protected boundaries.

3. RESULTS

3.1. General results

We analyzed three different ensemble forecasts (standard, climatic and landscape models) to evaluate the habitat suitability for WLP. The standard model (using all the environmental variables together) showed a large prevalence of suitable areas in forest regions of the country and less suitable areas in the central region where there is a predominance of landscapes altered by agriculture crops in the Cerrado biome. In the Caatinga, northeastern region of the country, and in the extreme south of the country, within the Pampas biome, the model showed lower habitat suitability for the species. The total area of 4,827,524 km^2 was predicted as suitable using the standard binary model. The AUC values ranged between 0.677 and 0.810, and the minimum sensitivity thresholds ranged between 0.014 and 0.455, among the four algorithms tested in the standard model (Table 1).

Table 1 - Thresholds and AUC average values from the habitat suitability models for *Tayassu pecari*.

Algorithm	**N**	**threshold**	**AUC**
Standard Model			
Bioclim	10	0.031	0.677
Gower	10	0.455	0.720
MaxEnt	10	0.264	0.810
SVM	10	0.014	0.733
Climate Model			
Bioclim	10	0.141	0.599
Gower	10	0.727	0.524
MaxEnt	10	0.400	0.703
SVM	10	0.014	0.619
Landscape Model			
Bioclim	10	0.046	0.669
Gower	10	0.459	0.698
MaxEnt	10	0.371	0.779
SVM	10	0.014	0.630

The climatic model and the landscape model produced divergent predictions for WLP in many regions of the country, showing that climatic and landscape models can provide complementary information for habitat suitability analysis (Figure 3). The total suitable area predicted with the climatic model was 6,414,900 km^2 and the total area predicted by the landscape model was 5,098,869 km^2. Both models estimated areas with larger extents and smaller AUC values than the standard model predictions in which we used all the variables together.

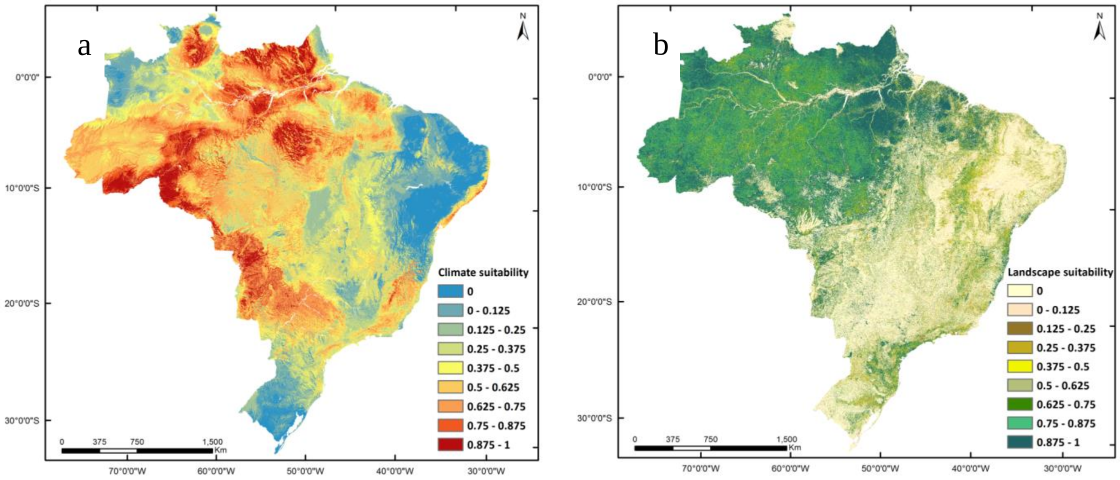

Figure 3. Climatic (a) and Landscape (b) models of habitat suitability for white-lipped peccaries (*Tayassu pecari*) in Brazil.

Besides the differences in the AUC values, the territorial extent of suitable areas for the species was different depending on the algorithm used. Model predictions made with the Bioclim and Gower models resulted in larger suitable areas than the model predictions made with the other two algorithms (MaxEnt and SVM). Additionally, AUC values were lower for Bioclim and Gower than values for MaxEnt and SVM (Table 1). We have also calculated the consensus areas predicted by all the standard models, which encompass 2,489,205 km^2 (Supplementary material).

Evaluation of the variables' importance according to results of the MaxEnt models using the jackknife of regularized training gain showed that the percent tree canopy cover, precipitation of the driest quarter (BIO17) and mean temperature of the warmest quarter (BIO10) were the most important variables for the species' habitat suitability (Figure 5). Although the explanatory importance for the suitability was concentrated on those three variables, the variance for each environmental variable (tested using the scaled values of the variables tested associated with the occurrence data) show distinct contribution and importance for each biome group in the principal component analysis (Figure 6).

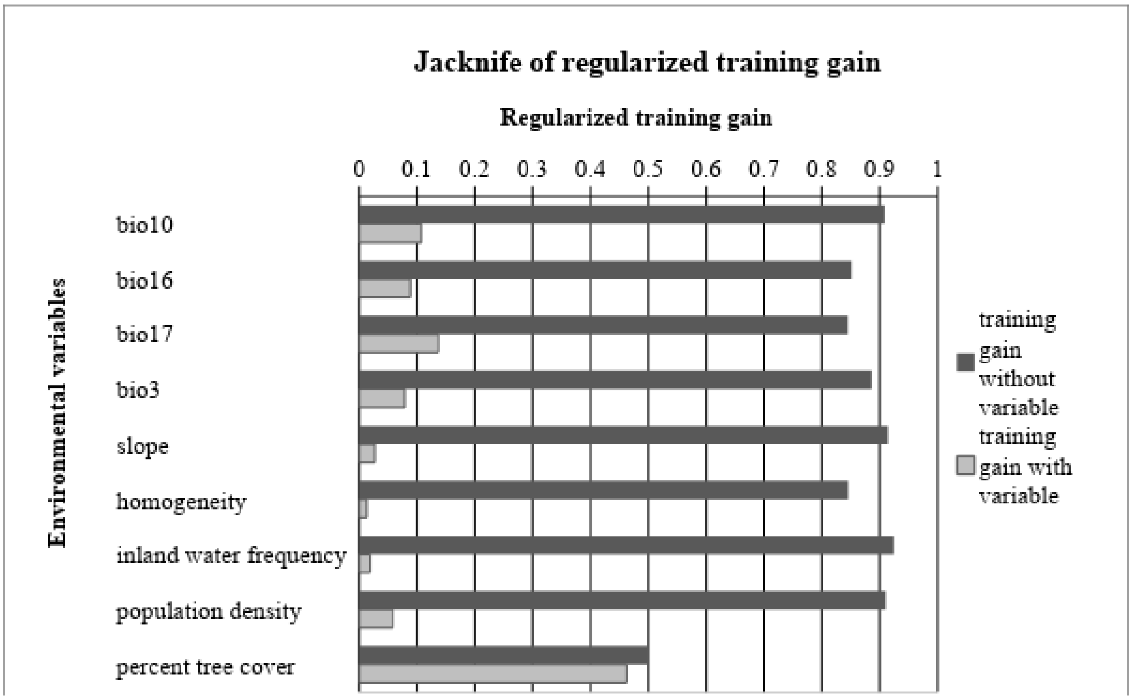

Figure 5. Jacknife training gain for MaxEnt models of habitat suitability for white-lipped peccaries (*Tayassu pecari*) in Brazil.

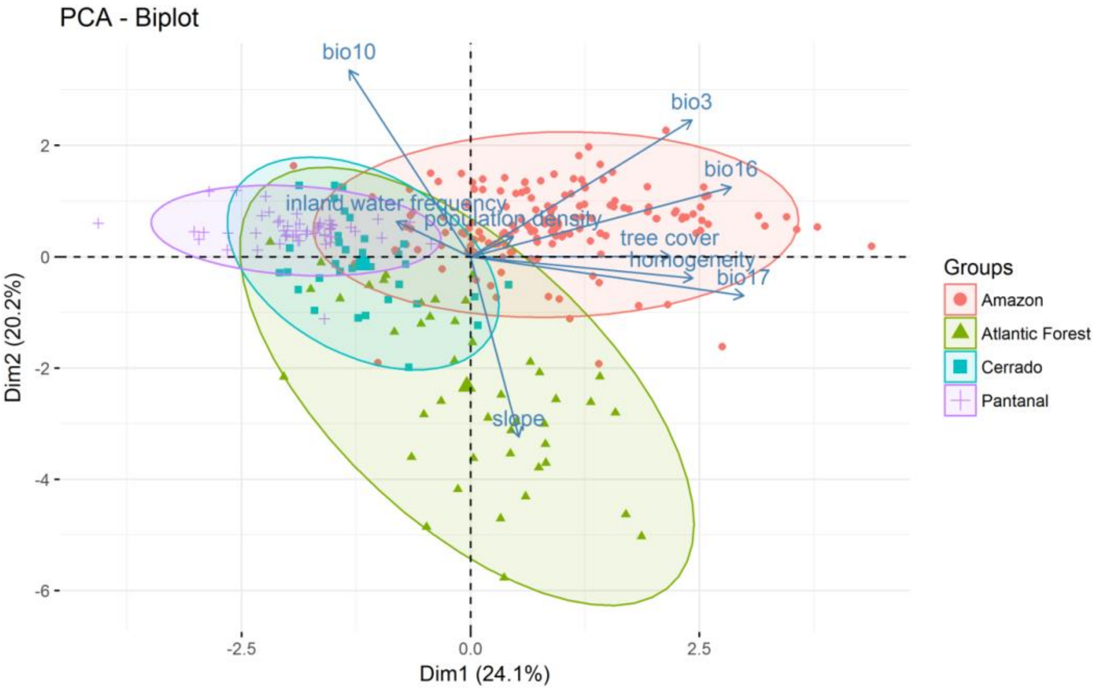

Figure 6. Principal Component Analysis using the environmental variables (percent of tree cover, homogeneity, inland water frequency, terrain slope, human density, isothermality - BIO3, mean temperature of warmest Quarter - BIO10, precipitation of wettest quarter - BIO16, precipitation of driest quarter - BIO17) values associated with the presence records used in the habitat suitability models for white-lipped peccaries (*Tayassu pecari*) in Brazil.

3.2. Summed model results

The summed model (*Ecoland approach*) allowed for comparisons about how climatic and landscape variables can provide different estimates of suitable areas. Although the estimates of separate categories of predictors provided broader extensions, the final summed model identifies specific regions where climatic and landscape conditions were critical or favorable for peccaries' persistence. We identified four categories of suitable areas from the summed model (Figure 4). Areas with higher suitability for both, the climatic and the landscape suitability models represent an extension of 2,981,024 km^2 (35% of the total area of Brazil; Figure 4: value = 1, red color**)**. Areas most affected by habitat loss and anthropogenic alteration represent an extension of 857,375 km^2 (10% of the total area of Brazil, Figure 4: value = 0.75, orange color). Such areas could be targets for restoration and corridor development since they present high climatic suitability values and medium/low current landscape suitability.

We also identified areas where landscape suitability was high but climatic suitability was low in the south, northeast and some specific regions of the Amazon, with an extension of 1,433,873 km^2 (17% of the total area of country; Figure 4: value = 0.25, green color). Finally, areas with low climatic suitability and low landscape suitability encompass 3,097,932 km^2 (37% of the total area of country; Figure 4: value = 0, blue color) of Brazilian territory, these areas present a predominance of shrubland vegetation and dry rainfall regime in the northeast (Caatinga), areas of grassland and low seasonal temperature in the south (Pampas), and areas with high land-use change, used mainly for agriculture within the "dry diagonal" in the center of the country (Cerrado).

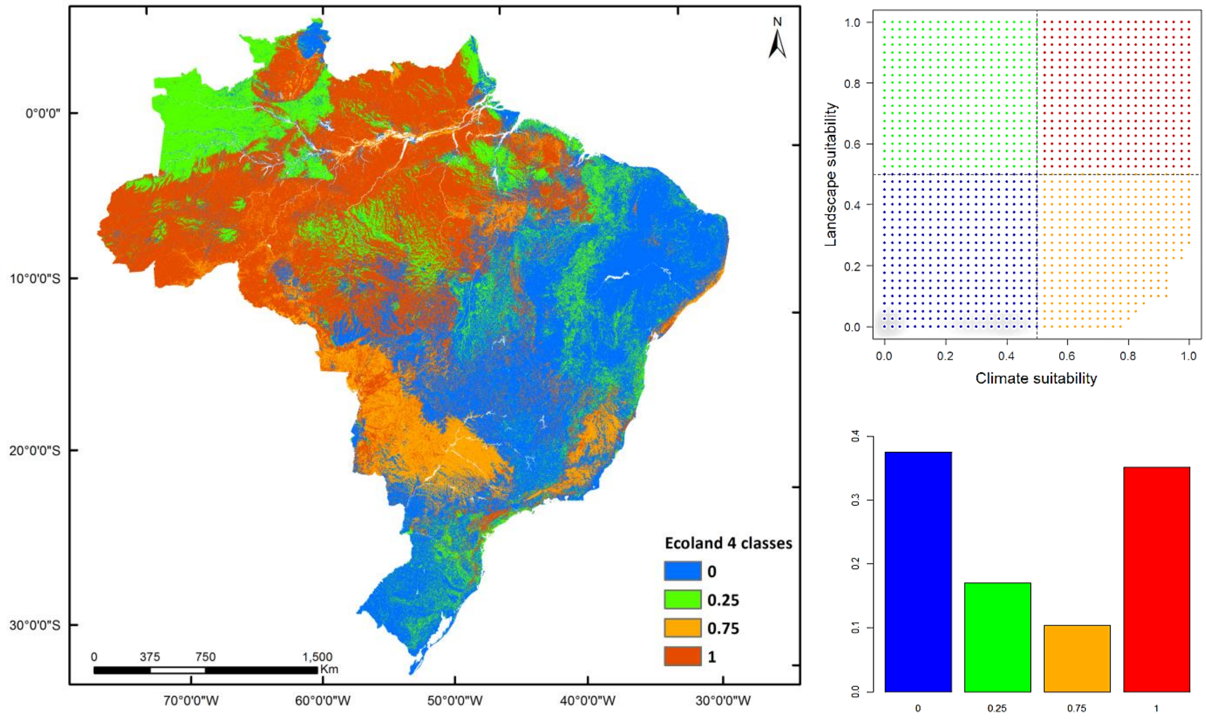

Figure 4. Summed model of climatic and landscape suitabilities for white-lipped peccaries (*Tayassu pecari*) in Brazil.

3.3. Suitable functional forest fragments results

In our last analysis to estimate functional suitable areas, we excluded all fragments smaller than 2050 ha (or 20.5 km^2) and also evaluated the impacts of forest loss between 2000 and 2016 (Figure 7). Filtering out fragments smaller than 2050 ha reduced suitable areas from 4,827,524 km^2 to 4,370,885 km^2. Furthermore, forest cover loss between 2000 and 2016 removed a total of 337,318 km^2 of suitable areas larger than 2050 ha. Both steps (spatial and historical filters) resulted in a reduction for 4,033,567 km^2 of suitable areas or 47% of the Brazilian territory. The functional suitable areas estimated per biome varied between 53,712 km^2 for the Pantanal and 1,932,735 km^2 for the Amazon, but the biome with the smallest proportion of suitable areas for WLP (20.2%) was the Cerrado (Table 2).

Table 2. Area and percent cover suitable functional forest fragments (higher than 2050 ha) for white-lipped peccaries (*Tayassu pecari*) affected by forest loss between 2000 and 2016 in Brazil.

Forest loss in suitable fragments (bigger > 2050 ha)	**km^2**	**%**
unsuitable area	3943974.7	46.4
suitable area > 2050 ha without forest loss	4033567.8	47.4
forest loss in unsuitable areas until 2016	186960.3	2.2
forest loss in suitable areas > 2050 ha until 2016	337318.2	4.0
Amazon	**km^2**	**%**
unsuitable area	665407.0	23.1
suitable area > 2050 ha without forest loss	1932735.3	67.0
forest loss in unsuitable areas until 2016	48426.9	1.7
forest loss in suitable areas > 2050 ha until 2016	239677.1	8.3
Cerrado	**km^2**	**%**
unsuitable area	1486187.5	72.9
suitable area > 2050 ha without forest loss	411527.1	20.2
forest loss in unsuitable areas until 2016	80029.9	3.9
forest loss in suitable areas > 2050 ha until 2016	62222.5	3.1
Atlantic Forest	**km^2**	**%**
unsuitable area	801554.9	71.8
suitable area > 2050 ha without forest loss	259008.0	23.2
forest loss in unsuitable areas until 2016	28836.7	2.6
forest loss in suitable areas > 2050 ha until 2016	27639.8	2.5
Pantanal	**km^2**	**%**
unsuitable area	91909.9	60.8
suitable area > 2050 ha without forest loss	53712.3	35.6
forest loss in unsuitable areas until 2016	2941.9	1.9
forest loss in suitable areas > 2050 ha until 2016	2489.3	1.6

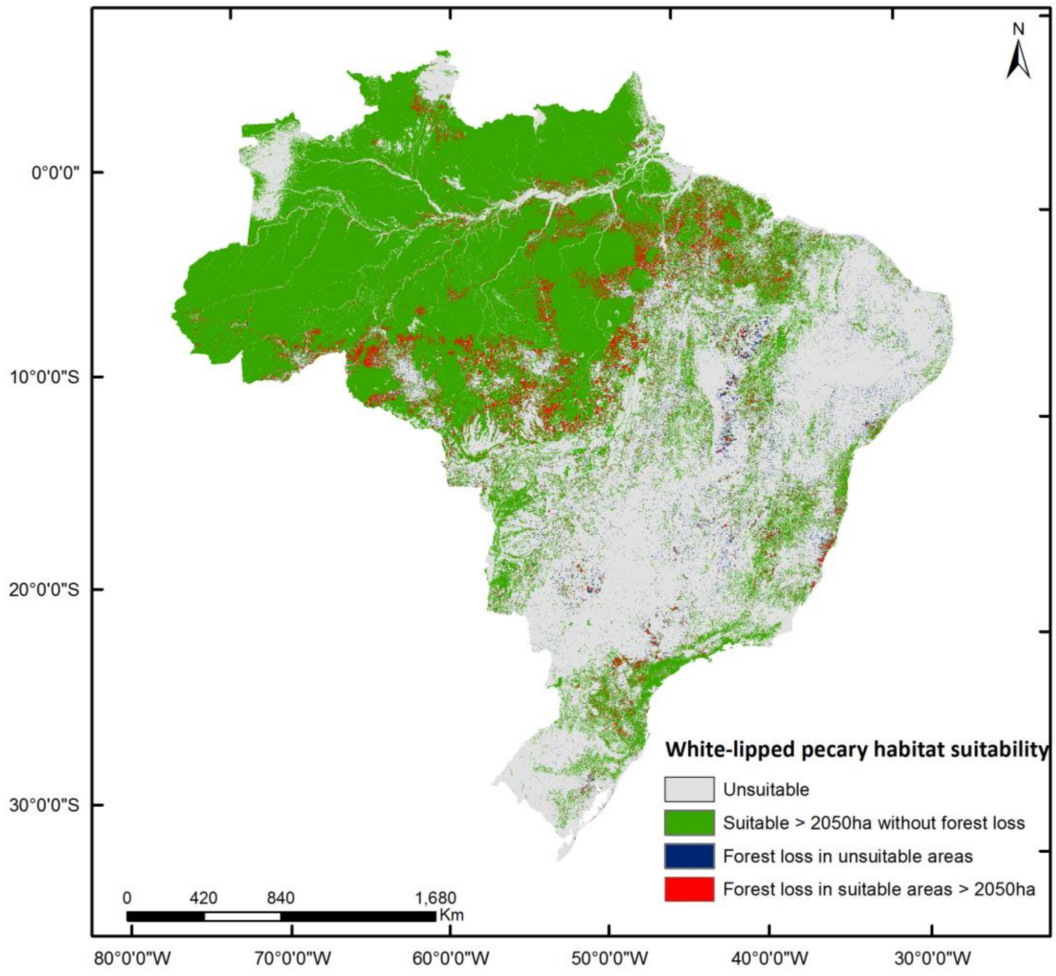

Figure 7. Effects of forest loss between 2000 and 2016 in suitable functional forest fragments (higher than 2050 ha) for white-lipped peccaries (*Tayassu pecari*) in Brazil.

Finally, the total extension of functional suitable areas located inside protected regions was 1,105,422 km^2 (Table 3**)**. In terms of extension, the proportion of protected areas holding suitable areas for WLP is higher in the Amazon biome, where 90% of protected regions are suitable for the species, and the Cerrado is again the biome where only 22% of the protected areas extensions are suitable for WLP.

Table 3. Area and percent cover suitable functional forest fragments (higher than 2050 ha) for white-lipped peccaries (*Tayassu pecari*) inside protected areas that were affected by forest loss between 2000 and 2016 in Brazil.

Suitable functional areas in protected areas	km^2	%
unsuitable inside protected areas	307668.5	21.3
suitable > 2050 ha without forest loss inside protected areas	1105422.0	76.4
forest loss in unsuitable areas until 2016 inside protected areas	9592.8	0.7
forest loss in suitable areas > 2050 ha until 2016 inside protected areas	24571.6	1.7
Amazon	**km^2**	**%**
unsuitable inside protected areas	88567.0	7.9
suitable > 2050 ha without forest loss inside protected areas	1007064.6	90.2
forest loss in unsuitable areas until 2016 inside protected areas	2274.0	0.2
forest loss in suitable areas > 2050 ha until 2016 inside protected areas	18856.1	1.7
Cerrado	**km^2**	**%**
unsuitable inside protected areas	113269.2	72.9
suitable > 2050 ha without forest loss inside protected areas	34389.5	22.1
forest loss in unsuitable areas until 2016 inside protected areas	4407.8	2.8
forest loss in suitable areas > 2050 ha until 2016 inside protected areas	3392.0	2.2
Atlantic Forest	**km^2**	**%**
unsuitable inside protected areas	43122.6	46.4
suitable > 2050 ha without forest loss inside protected areas	46905.2	50.5
forest loss in unsuitable areas until 2016 inside protected areas	1170.3	1.3
forest loss in suitable areas > 2050 ha until 2016 inside protected areas	1751.4	1.9
Pantanal	**km^2**	**%**
unsuitable inside protected areas	2533.4	50.7
suitable > 2050 ha without forest loss inside protected areas	2419.1	48.4
forest loss in unsuitable areas until 2016 inside protected areas	12.3	0.2
forest loss in suitable areas > 2050 ha until 2016 inside protected areas	31.6	0.6

4. DISCUSSION

Understanding the distribution of remaining suitable areas that can favor the persistence of WLP populations is an important step to establish conservation plans for the species, other forest-dwelling vertebrates, and the maintenance of forest function. Evaluating and identifying areas where forest loss is affecting suitable habitats is also essential to assess the conservation status for the species regionally. Identifying potential corridors and priority areas for restoration in fragmented landscapes based on the species requirements will be essential to ensure the movement permeability and gene flow between remaining populations, especially in the Cerrado and Atlantic Forest biomes where defaunation, habitat loss, and habitat fragmentation are increasingly affecting the distribution of all wide-ranging neotropical forest species (Galetti et al., 2017; Jorge et al., 2013 Carvalho et al., 2009; Ribeiro et al., 2009)

4.1. Potential implications of the summed model results for WLP conservation

We applied the summed model to identify areas that would require different conservation action prioritization. Orange areas (high climatic suitability-low landscape suitability) can be targets for restoration and corridor construction, promoting greater landscape suitability and connectivity where climatic conditions are favorable. Moreover, these regions are also important ecotones and can strategically favor gene flow between populations across different biomes. Recent studies show that large mammals, including WLPs, can occupy secondary savannahs regenerated from clear-cutting in areas of protected Cerrado, suggesting a potential reversal of the non-habitat matrix to suitable habitats not only for WLPs, but for other forest-dwelling species occupying regenerated landscapes (Ferreira et al., 2017).

The red areas of the summed model represent forests with highest suitability in terms of both climate and landscape context, and it is critical that they remain protected and connected by environmental laws, such as the Brazilian Forest Code (Azevedo et al., 2017; Soares-Filho et al., 2014), and deforestation monitoring through remote sensing coupled with ground truth inspections. National programs such as Mapbiomas (http://mapbiomas.org) and the “SiCAR” system (Sistema Nacional de Cadastro Ambiental Rural) (Alix-Garcia et al., 2018) can help identify private properties where deforestation is occurring to apply appropriate fines whenever necessary. It is also important to create new protected areas in priority regions to enhance connectivity and enforce surveillance to avoid illegal hunting and deforestation. Besides these goals that include national initiatives, environmental education is important to reduce illegal hunting locally and regionally in the biomes where the species is largely threatened - Atlantic Forest and Cerrado (Keuroghlian et al., 2013).

The green areas in the summed model have low current climatic suitability and high landscape suitability. They should be monitored especially for climate change effects. As already discussed by Keuroghlian et al. (2015), increased drier climates can affect resource availability, change activity patterns (Hofmann et al., 2016), and increase the impacts of land-use change. It is predicted that synergetic effects of climate change and land use change will increase species losses in tropical savannahs, grasslands and forests, and result in significant alteration in the structure of ecological communities by 2070 (Newbold, 2018). In the green areas of our final model, WLP populations are likely strongly affected by climate change and rely on appropriate landscape suitability to survive.

Although the species' historical ecological distribution (Altrichter et al., 2012) suggests that WLPs exhibit considerable plasticity in habitat use, from a macroecological perspective such plasticity is climatically restricted to the warmer regions of the neotropics. Conservation strategies are critical for retaining suitable forest fragments for the species in areas where climatic suitability is high, since range shifts in climate change adjustments can be prohibitive for medium and large mammals, including evolutionary adjustments with phenotypic plasticity (Hetem et al., 2014). This is further hindered by land-use change and anthropogenic barriers that limit movements and dispersal of organisms (Shepard et al., 2008).

4.2. Forest loss implications for WLP conservation

WLPs can be detected in open environments such as native grasslands and some shrublands, but depend mostly on forest areas to acquire food resources (Desbiez et al., 2009; Keuroghlian and Eaton, 2008a) and to reduce thermoregulation costs (Hofmann et al., 2016). Therefore, increased patch isolation contributes to reduce population viability especially when the matrix restricts movement of individuals (Prevedello and Vieira, 2010; Revilla and Wiegand, 2008). However, studies that show how different matrix types and qualities affect forest ungulate movements are still lacking. Furthermore, reduction in patch area and forest cover could also increase forest disturbance caused by edge effects and facilitate human access. The combination of patch size reduction with isolation can also increase inbreeding for WLP (Biondo et al., 2011). The total suitable area affected by forest loss in Brazil between 2000 and 2016 (337,318 km^2) is larger than the current range predicted for the species in most countries of Central America (Altrichter et al., 2012).

Our suitability maps for WLP also reflect how land-use change has evolved in different regions of Brazil. In the biomes where the conservation status of WLPs is currently considered less critical - Pantanal and Amazon (Keuroghlian et al., 2013), much of the forest loss affects the edges of the biomes and most of the land conversion is used for cattle-ranching. However, reduced human density and reduced access through roads (Oliveira et al., 2016) helps prevent larger anthropogenic impacts in those regions. In the Cerrado, expansion of cropland and cattle-ranching are the main land-use changes. Moreover, in some regions of the Cerrado, the matrix consists of cropland that is attractive to WLP (soybean and corn), which can increase human conflicts and consequently illegal hunting pressure and human/wildlife conflicts near forest fragments (Lima et al., 2018). One example is Emas National Park, where the main surrounding areas consist of maize monoculture (Jácomo et al., 2013) and there has been increased human-WLPs conflict in the area. In the Atlantic Forest, in addition to higher human density in urban areas near the coast, there is a predominance of large tracts of forest fragments in coastal areas, especially in high-elevation areas in the Serra do Mar and Mantiqueira mountain ranges. Interior regions of the Atlantic Forest have smaller and more isolated forest remnants (Ribeiro et al., 2009) and some of the remaining WLP populations are very isolated (Keuroghlian et al., 2004). WLPs are already absent from many protected areas (Jorge et al., 2013) which can generate cascading effects on plants and animals (Galetti et al., 2015; Kurten, 2013).

4.3. Other anthropogenic effects that impact WLP populations

Our models were able to show the broad scale impacts of forest loss and fragmentation, climate and direct human disturbance (human density) on the spatial distribution of suitable areas for WLPs in recent years. Nevertheless, the conservation scenario is more problematic due to other human-driven disturbances, like increasing human activities - light and sounds for example - which have been shown to alter the activity patterns of mammals (Gaynor et al., 2018), create barriers (Shepard et al., 2008), increase poisoning and slaughtering because of human/wildlife conflicts (Lima et al., 2018) and increase hunting pressures (Peres et al., 2016), occurring on the landscape and local scales within forest fragments. These local impacts can highly increase biodiversity loss even where forested areas still remain (Barlow et al., 2016; Galetti et al., 2017; Peres et al., 2016), which could be the case for many regions where the WLPs occur.

Anthropogenic impacts within forests can increase the loss of biodiversity (Barlow et al., 2016; Betts et al., 2017) and to evaluate the synergistic effects of habitat loss and other anthropogenic impacts require monitoring of other compositional and population parameters for forest-dwelling mammals. This would allow for more precise evaluation of the implications in the population level at a local scale, such as mortality rates and survival. For social species such as WLP, parameters such as abundance, group size and biomass are also important conservation indicators (Altrichter et al., 2012; Keuroghlian et al., 2013; Reyna-Hurtado et al., 2016).

4.4. Protected areas and conservation strategies to reduce the impact of forest loss for WLP

Models that predicted habitat suitability for WLP at the landscape scale showed that the presence of protected areas was a very important variable to explain the areas that were most frequently used by WLPs (Norris et al., 2011). Our results show that even inside protected areas, the proportion of suitable areas, *i.e.* fragments larger than 2050 ha, represents only half of the territory of protected lands in the Pantanal and Atlantic Forest, and even less in the Cerrado (22%). Therefore, even within protected areas, there are large portions that are unsuitable for WLPs.

The recent changes in legislation that protect the forest fragments in Brazil reduced the extent of areas that should be protected near rivers, therefore riparian vegetation and small remnants could be further reduced in the near future (Soares-Filho et al., 2014), which are important habitats for WLP (Keuroghlian and Eaton, 2008b). Furthermore, applying sustainable agricultural production strategies that minimize forest reduction, such as rotation management systems for cattle and crop production - reducing area requirement and the impact on native trees (Esquivel et al., 2008), encouragement for programs of payment for ecosystem services (Pearce, 2001), compliance of the forest code as a criteria for marketing, as well as the use of green certificates for exportation of rural products and reduction of meat consumption (Eisler et al., 2014), will be essential to decrease the impact of food production on white-lipped peccaries and other wild species (Phalan et al., 2011).

4.5. Model limitations and conclusions

We are aware that our models have some limitations; suitable areas are overestimated for the species since we used a resolution of 1 km^2, because the edges and the shapes of fragments loose definition on broader scales. Nevertheless, although highest resolution could provide a more accurate estimate, our predictions provide the best current overview of the status of suitable areas for WLPs in a country with continental dimensions and a myriad of environments. The use of the four different algorithms allowed for more accurate comparisons of the suitable areas and determination of uncertainty between predictions, indicating regions where more information about the species occurrence could improve model's prediction (Supplementary material).

Testing two different modeling approaches and a range of different environmental variables was important for selecting the final set of variables. We observed that distance from forest edges, which is connected to distance from river banks in the Amazon region, and also from roads in other biomes, were predictors that limited the distribution of suitable areas (Supplementary material), meaning that higher values of suitability were observed in more accessible areas in the tested models with those variables included. Although distance from water resources could be a meaningful variable to explain the WLP habitat suitability in finer resolution models of home range and landscape scale (Ferreira et al., 2017; Keuroghlian and Eaton, 2008b; Reyna-Hurtado et al., 2009), higher probabilities of detection for WLP near rivers most likely influenced our model prediction for the Amazon, and as a result, we observed an over-fitted model. Therefore, we excluded distance variables from the final estimates. It has already been shown that biodiversity data for the Brazilian territory is mostly biased by detection through access routes (Oliveira et al., 2016). Therefore, new survey efforts in the Amazon and continued monitoring could help to increase the understanding of WLP presence and distribution in the region, especially in the areas where uncertainty was high (Supplementary material).

Our results represent an important step in evaluating the remaining suitable areas that currently exist for WLPs in Brazil because they provide spatial information about how landscape modifications and anthropogenic pressure is affecting the species persistence. This is essential to evaluate the species current conservation status and to define more efficient conservation actions, such as new areas for population surveys and monitoring, placement of corridors and target regions for educational programs that seek to reduce habitat loss and illegal hunting. Finally, our models showed that WLPs respond to landscape changes and have been losing habitat in recent years, therefore applying national conservation strategies using WLPs as a landscape species could optimize conservation efforts for other mammal species with similar sensitiveness to fragmentation.

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III CHAPTER 2

Planning my next step: how landscape variables influence movement decisions of a forest ungulate within tropical landscapes?

ABSTRACT

In this study, our aim was to investigate how the landscape structure (land cover variables, patch size, distance from fragment edge, water sources distribution, topography, and anthropogenic impacts) could affect movement decisions and habitat selection for a neotropical forest ungulate, the white-lipped peccary - *Tayassu pecari* (WLP). WLPs are social ungulates that form the most important biomass of mammals in the Neotropical forests where they still exist. We hypothesize that WLP movement and habitat selection would be positively influenced by the increase of forest cover, percent of tree cover, patch size, and water availability. In contrast, variables related to anthropogenic impact would repel WLP, thus the individuals monitored would avoid areas closer to roads, human population or higher densities of people. From July 2013 to October of 2016, we have tracked 30 individuals from 10 herds (~2 inds./herd), 4 herds in the Pantanal wetlands and 6 herds in the Cerrado highlands of Mato Grosso do Sul. Twenty four individuals had at least one month of data and we regularized their tracks to get 4 fixes per day (6 hour interval) to apply Step Selection Analysis. Our main results showed a positive selection of WLP for natural vegetation and forest areas when compared with the matrix composed mainly by pasture. A higher percent of tree cover, larger forest patches, proximity to water sources and proximity with fragment center had a positive effect on habitat selection. WLP avoided steep slope areas, paved roads, and areas of higher population density. Individual and herd variation was detected in the step selection response. Maximum gap crossing of matrix pasture areas did not exceed 700m. Our results showed that functional connectivity for WLP can be limited by land cover, roads and highly populated regions and this information can be applied to determine new conservation management actions in our study region.

Keywords: habitat selection, step selection, fragmentation, anthropogenic impacts, connectivity.

1. INTRODUCTION

Movement is a fundamental ecological process that is directly or indirectly connected with biodiversity composition, resource selection and gene flow by animals and plants (Jeltsch et al., 2013; Nathan et al., 2008). As movement can be measured and can affect animal and plants in different spatial and temporal scales (Benhamou, 2014), it can be incorporated in different models to investigate what are the main mechanisms that determine navigation, migration, home range and habitat selection (why animals choose some areas to live) and dispersal (why animals choose specific routes for displacement) (Gurarie et al., 2016; Morales et al., 2004; Nathan et al., 2008; Schick et al., 2008). The movement patterns that animals evolve are part of a complex system that is composed by their movement capacity and also by internal and external factors affecting their individual choices in every step, day, season and year of their lives (Nathan et al., 2008).

Current advances on the technology to track wildlife provided new possibilities to collect and analyze movement data in a high frequency, during all the periods of the day, in regions of difficult access to humans and through different seasons of the year (Cagnacci et al., 2010). GPS technology improved animal monitoring, when compared with VHF telemetry, because it also allowed scientists to observe and track animals’ movement decisions with less interference in their behavior since the satellite transmission of the movement data does not require a human observer in the field (Cagnacci et al., 2010; Cooke et al., 2004; Moorcroft, 2012). Summed up with the new products available from remote sensing techniques, it is now possible to explore how those movements are affected by changes in the environment and by anthropogenic impacts in a finer scale of analysis (Fortin et al., 2005; Pettorelli et al., 2014).

Such fine scaled information provides new insights about habitat selection (Beyer et al., 2010; Fieberg et al., 2010), home range establishment (Börger et al., 2008; Fieberg and Börger, 2012; Fleming et al., 2015; Moorcroft, 2012), and can be used for conservation purposes such as identifying how animals are responding to disturbances and finding key habitats (Thurfjell et al., 2014), fundamental elements to determine management actions and protected areas. Although it is still a challenge to deduce ecological processes from individual observed patterns (Tyre et al., 2001), the investigation of how spatial structure can facilitate or create barriers to animal movement is an important first step to understand how more complex ecological processes are affected by movement decisions (Fortin and Dale, 2005; Holyoak et al., 2008; Nathan et al., 2008).

Some species of animals and plants can be rapidly affected by alterations in the landscape configuration and composition because these changes can alter connectivity and the total habitat amount available for them (Pardini et al., 2017; Prugh et al., 2008), two important landscape characteristics already known to affect species distribution and habitat selection (Fahrig, 2007; Jorge et al., 2013; Newbold et al., 2015; Pardini et al., 2017). The impacts of landscape alteration, especially with forest loss and fragmentation, can cause reduction on the abundance or even local extinction of more sensitive species (Galetti et al., 2017; Jorge et al., 2013; Keuroghlian et al., 2015; Paviolo et al., 2016) or simply alter their movement patterns (Tucker et al., 2018), especially for mammals that are forest specialists rather than generalists (Beca et al., 2017; Lyra-Jorge et al., 2010; Magioli et al., 2015; Pardini et al., 2017; Rocha et al., 2018).

In this study our aim was to investigate how the landscape structure (land cover variables, patch size, distance from fragment edge, water sources distribution, topography, and anthropogenic impacts) could affect movement decisions and habitat selection for a neotropical forest ungulate, the white-lipped peccary - *Tayassu pecari* (WLP) (Link, 1795) which is one of the three extant recognized species of the Tayassuidae family in the New World Cetartiodactyla. This species was chosen to be our model species because of its peculiar behavior characteristics and important ecological role in the Neotropical forests, where it is currently classified as Vulnerable (IUCN Red List) as consequence of habitat loss, fragmentation, hunting, competition with livestock, and emerging diseases (Altrichter et al., 2012; Beck, 2006; Keuroghlian et al., 2013; Peres, 1996; Reyna-Hurtado, 2009). WLPs are social ungulates that form the most important biomass of mammals in the Neotropical forests where they still exist (Beck, 2006; Eisenberg, 1980; Peres, 1996). They are also important seed predators and dispersers (Beck, 2006; Keuroghlian and Eaton, 2008b) and prey for large carnivores such as jaguars (*Panthera onca*) and cougars (*Puma concolor*) (Cavalcanti and Gese, 2010; de Azevedo and Murray, 2007; Perilli et al., 2016). Therefore understanding how land-use change and anthropogenic impacts are affecting movement and habitat selection for the species is essential to guide conservation management actions regionally.

More specifically our aim was to answer some specific questions:

1. *What is the gap crossing capacity for the species in the studied region?*

We hypothesize that WLP will have some matrix permeability limitation, and they will avoid crossing large distances within the matrix, which in our area is mainly composed by pasture. A distance limitation to matrix crossing can indicate a behavior response of exposition avoidance, which can be a good indicator of avoidance of risks in the matrix.

2. What are the main landscape variables that influence movement decisions and habitat selection for WLPs in the Pantanal and Cerrado of Mato Grosso do Sul state?

We hypothesize that WLP movement and habitat selection will be positively influenced by the increase of forest cover, percent of tree cover, patch size, and water availability. In contrast, variables related with anthropogenic impact will repel WLP, thus the individuals monitored will avoid areas closer to roads, and human population or higher densities of people, we also hypothesize that WLP will avoid using areas far away from the forest, which was already explained previously. Slope and drainage must play an important role for the selected areas by WLP mainly in the Cerrado region because remaining forests areas are generally associated with higher slope values in more fragmented landscapes. Inland water must play an important role for the selected areas mainly in the Pantanal region where the alluvial plain dynamics is more effective in shaping the landscape.

2. MATERIAL AND METHODS

2.1. Study species

WLP occur along different environments distributed through the Americas, more specifically from southeastern Mexico to northern Argentina and southern Brazil, occupying forests, savannahs, and wetlands (Beck et al., 2017; Sowls, 1984). This species occurs in different ecoregions of Latin America but they are mainly forest dependents (Hofman et al., 2016; Jorge et al., 2019; Keuroghlian and Eaton, 2008a; Peres, 1996; Reyna-Hurtado et al., 2009). As a frugivore-omnivore species, the WLP has an important ecological role particularly predating fruits, plants and dispersing seeds (Keuroghlian and Eaton, 2008b). WLPs are considered as ecosystem engineers because of the new habitats created by their secondary impacts on forest vegetation while moving, trampling on seedlings and resting in their most used trails and sleeping sites (Beck, 2006; Beck et al., 2010; Keuroghlian and Eaton, 2009, 2008b; Kiltie and Terborgh, 1983). This species is highly social, living in herds that can have more than100 individuals of both sexes all age classes (Biondo et al., 2011). Herds social organization is characterized by fission and fusion dynamics with frequent individuals exchange among subherds (Biondo et al., 2011; Keuroghlian et al., 2004). The home range of a single herd can vary in size from 15 to 200 km^2 (Bodmer, 1990; Carrillo et al., 2002; Fragoso, 1998; Hofman et al., 2016; Jácomo et al., 2013; Jorge et al., 2019; Keuroghlian et al., 2004; Kiltie and Terborgh, 1983), therefore WLP is good surrogate species of habitat quality since they need large and well-preserved forests to live.

2.2. Study area

The Pantanal is referred as one of the largest freshwater wetlands in the world, located in the central portion of South America (16–20°S and 55–58°W) in the Upper Paraguay River Basin (UPRB), and encompassing 160,000 km^2 of total extension if we consider Brazil, Bolivia and Paraguay territory from this about 140,000 km^2 the Brazilian area (Alho, 2005; Alho et al., 1988; Junk et al., 2006). It is also considered a UNESCO World Biosphere Reserve for being a wildlife hotspot and to shelter endangered species (Harris et al., 2005). This lowland environment, with 80 to 200 m of altitude, is characterized by the interaction among distinct alluvial systems, as fluvial megafans, interfan river plains and lakes (Assine et al., 2015), where the river channels are very dynamic and can change their position suddenly (Assine and Soares, 2004; Pupim et al., 2017).

The climate of the Pantanal is a savanna climate with a dry season from May to September and a wet season from October to April (Junk et al., 2006; Por, 1995). The mean annual precipitation ranges from 1000 mm within the basin to 1500 mm on the uplands in the east and north. The mean annual temperature is around 25 ^oC, but it can highs up to 40-45 ^oC during the summer and the evaporation is higher than the precipitation during most of the year (Alho, 2005; Por, 1995). The monsoonal behavior of the rainfall strongly controls river discharge, causing the flood-pulse phenomena along the floodplain (Junk and Nunes De Cunha, 2005), where large sectors of the Pantanal floodplain are submerged from 4 to 8 months each year by water depths varying from a few centimeters to more than 2 m (Marengo et al., 2016).

The spatial distribution of vegetation formations in largely influenced by the local topography, seasonal flooding and soil type (Prance and Schaller, 1982). The non-flooded vegetation (mainly Cerrado forest) occurs on well-drained sandy soils related to local ridges (1 - 5 m) that are free of seasonal flooding. Whereas, the flooded vegetation occurs on clayey eutrophic soils related to seasonal swamps and floodplains with the development of gallery forests, scrubs and grasslands (Pott and Pott, 2004). This complex interplay between physical and biological aspects is fundamental to drive regional ecological processes and result in a complex heterogeneous landscape.

The Pantanal lowlands are surrounding by low-altitude Cerrado plateaus (<1000 m) and a dense stream network resulting in dissected valleys with steep slopes. These plateaus are geomorphologically more stable than the lowlands and have been sculpted since the early Cenozoic (Assine et al., 2015). Cerrado forest was the predominant type of vegetation cover on the highlands, but during the last 50 years, nearly 60% was cleared and converted to cash crops or exotic (non-native) pasturelands (Roque et al., 2016; SOS Pantanal, 2015). The processes occurring in the upland regions of the river basins strongly influence processes occurring down-slope and downstream on the Pantanal floodplain (Padovani, 2010; Roque et al., 2016).

2.3. Capturing procedures

The capture process followed procedures described by Keuroghlian et al. (2004) and licenses were provided by the Brazilian National Environmental Agency following the rules for capture and immobilization of medium and large mammals (ICMBio - Instituto Chico Mendes de Conservação da Biodiversidade – SISBIO license n. 31088 and n. 46131). Temporary baiting stations were set up in areas that the peccaries use frequently, indicated by footprints and trail marks. Box traps (120 l x 90 h x 60 w cm) (Figure 1a) and wire mesh panel traps (Figure 1b) were placed at these stations and baited with salt, corn, yuca (*Manihot* sp.) and local fruits. We also monitored herd size and composition using camera traps in front of the trap, and we have attached VHF trap site trigger alarms from Telonics® to monitor and report for capture within a distance for the trapping sites. With this trigger alarms, we could check the status of various traps and reach the triggered trap faster once a WLP was captured.

Figure 1. (a) Box traps and (b) wire panel traps that will be used to capture white-lipped peccaries.

Once caught, the weight of the peccary was estimated and the individual was anesthetized in the trap with a TeleDart RD206 air-compressed injection pistol and a Dart 3 cc syringe with zolazepam–tiletamine (Zoletil50®, Virbac, Brazil, 0,9ml/10kg) (**Figure 3**). Captures and handling of sedated WLP were made with following WLP specialist and veterinary instructions (Figures 2a and 2b), which also checked the heart frequency of the anesthetized individuals and evaluated their health conditions.

Figure 2. (a) Veterinary checking individual heart frequency and (b) team making morphometric measurements during capture in Refúgio Ecológico Caiman, Pantanal.

Individuals were sexed, weighed, marked with a radiofrequency identification microchip in between the shoulder blades of each animal (PIT tag from Biomark®), and placed in an approximate age class based on tooth wear (Keuroghlian and Desbiez, 2010; Sowls, 1984). Morphology measures were taken as well as samples of fur and blood for DNA, isotopic and diseases analysis that were sent for collaborator researchers. After the biometric and collar procedures ended, animals were kept inside the traps for anesthetics' full recovery, and we released the animals six to twelve hours after sedation. Traps were covered to avoid animals to get stressed while recovering from the anesthetics. Individuals were VHF/GPS tracked after release and we could observe that they re-joined the herds through tracking, observations, and photos from camera-traps; sometimes the herd would stay close to the captured individuals and would only leave after they were released from the traps showing cohesive group behaviour.

2.4. Movement monitoring

We focused our capturing efforts and herds monitoring between 2013 and 2016 in private properties located in Mato Grosso do Sul state. In the plain, captures and monitoring were made in the municipalities of Miranda and Aquidauana, southern Pantanal wetlands, in four main areas with different landscape compositions at Fazenda 23 de Março, Refúgio Ecológico Caiman (with two main herds monitored in Caiman 1 and 2) and Fazenda Barranco Alto. The economic activities developed in those farms are mainly tourism and cattle ranching. In the plateau, we captured and monitored herds in six different areas in the municipality of Corguinho: one near the Taboco region and the other five at Fazendas Colorado, Jacobina, Santa Tereza, Safira, and Claudia. The main activity in the region is also cattle ranching.

Movements of white-lipped peccaries (WLP) were recorded with the GPS/VHF Iridium collars from Followit (Tellus Small total weight of collar ~660 g). We have deployed GPS collars on 30 individuals (Figure 3), one male and one female per herd preferentially, but we had more captures of adult females than males. Collars were programmed to receive 4 to 8 georeferenced positions (hereafter fixes)/individual/day for 12 months (365 days/individual). Data satellite transmission was made every two days during the monitoring and information about the WLP positions could be retrieved through web server from Followit. One individual (Malu) was monitored in two distinct periods because it was recaptured in different seasons, the first period of monitoring was between June and December of 2014, and the second between September of 2015 and March of 2016.

Collars were programmed to be automatically open through a drop-off system after 1 year. We used the Followit battery duration estimate to program the drop off, however not all the collars lasted until the drop off final programming so once they stop communicating via Iridium satellite we did field work campaigns to try to find the individuals with VHF monitoring and recover the GPS-collars with an alternative UHF activated' drop off system.

Individuals were monitored by radio tracking during 7 to 10 days during the field works that were held mainly in dry months. VHF signals were transmitted daily between 9 am to 3 pm to enable herds tracking, checking the collared individuals, resource consumption and herds composition visually during season fieldwork. Areas frequently used were visited to identify foraging and resting sites and to collect land-use data for ground truth data for mapping.

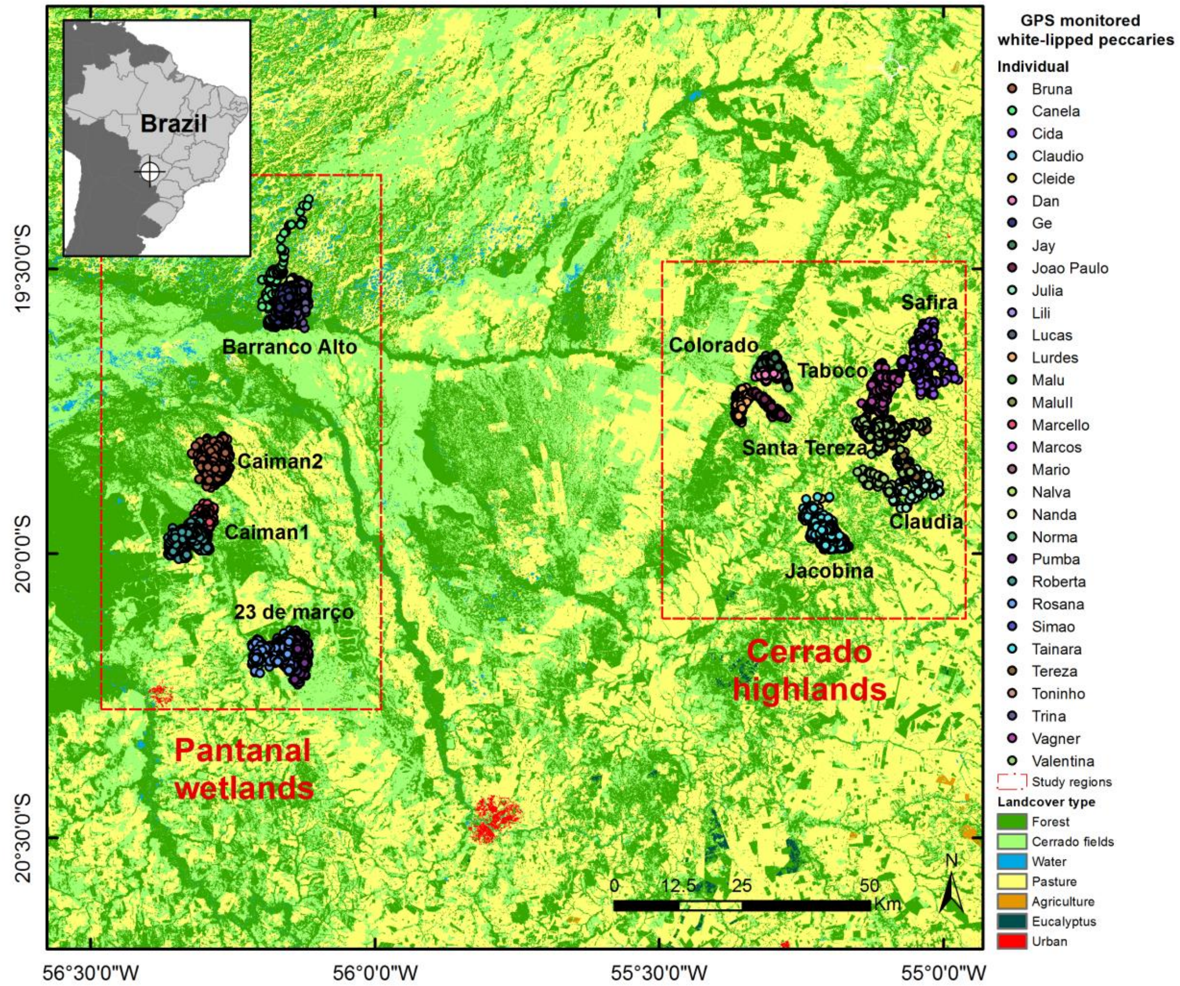

Figure 3. White-lipped peccary monitored with GPS radio collar in the study regions of the Pantanal and Cerrado highlands of Mato Grosso do Sul state.

2.5. Mapping (GIS) and landscape metrics calculation

Land cover information was based on the 2015 Mapbiomas Collections 1 and 2 datasets (Mapbiomas, 2016) to create simplified land cover map with categories (1- Forest, 2 – Other non-classified cover, 3 – Water, 4 – Natural non-forest vegetation (Cerrado fields), 5 – Pasture, 6 – Agriculture, 7 – Planted Forest, 8 – Coastal Zone vegetation, 24 – Urban). A second raster with only 3 categories was also created based on the Mapbiomas map and tested in the step selection function models (with 3 categories: forest (1), non-forest natural cover (4), matrix (other)).

Land cover classification from Mapbiomas was used to select all forest areas (categorie 1) from our study sites and to derive a raster of structural connectivity, considered here as the measurement of the *forest patch size* structurally connected, and *edge distance* raster for our study site. Distance from the boundary line between habitat - forest cover - and matrix (hereafter referred to as forest edge) was also calculated based on these patch classifications, using the edges as a zero line as the. Therefore distance had positive values in the matrix and negative values inside the forest patch. The size for the fragment patches and the distances from patch edges were calculated using GRASS GIS extension for connectivity from the Spatial Ecology and Conservation Laboratory (LEEC) - LSMetrics (https://github.com/LEEClab/LS_METRICS). We have also collected ground truth data during fieldwork to validate and correct the landcover classification.

Percentage of tree canopy cover and forest loss (from 2000 to 2015) was obtained in the Global Forest Change databank - https://earthenginepartners.appspot.com/science-2013-global-forest (Hansen et al., 2013). We have removed all the forest loss area and updated the percent tree canopy cover map for estimates that could reflect better the reality of forest cover for 2015.

Two anthropogenic layers were used as proxies for human disturbance and accessibility. One layer was based on the results of *human population density* information provided by the 2010 census from the Brazilian Institute of Geography and Statistics (IBGE, www.ibge.gov.br). We have downloaded the entire vector data containing the census results that are available in the IBGE ftp server, the data was then rasterized and a mosaic to a single raster (ftp://geoftp.ibge.gov.br/recortes_para_fins_estatisticos/grade_estatistica/censo_2010/). We have also transformed the information of human density in a raster of presence (1) and absence (0) of human population and calculated the euclidean *distance from the human population* presence areas. The second layer was *distance from paved road* which was based on the shapefile of existing roads, freely downloaded from the Departamento Nacional de Infra-estrutura de Transportes (DNIT, http://servicos.dnit.gov.br/vgeo/). After classifying the existent paved roads, we calculated the euclidean distance from the roads in all the Brazilian territory in ArcGIS 10.2.

Four variables related with water availability were tested in our models. We used the classification of water from Mapbiomas 2015 (categorie 3) and the water map publicly available at the Global Land Cover Facility (GLCF) website (http://glcf.umd.edu/data/waterfrequency/) which is based on the *inland surface water frequency* dataset (GIW) from Feng et al. (2016). We summed information from the two databases in a joint raster to create a map of water sources and then we have calculated the Euclidean *distance from the water* sources also in ArcGIS 10.2. The GIW is a global, high-resolution (30-m) inland water body dataset for 2000. This layer was also used separately to test the effects of seasonally inundated areas on suitable areas for the WLP, because especially in the Brazilian Pantanal, the effects of seasonal flooding are important to shape the dynamic landscapes and with the frequency information we can separate areas that are continuously or just seasonally flooded. We have also analyzed the effects of *distance from drainage* system and from main rivers in WLP step selection. Distance from drainage network and main rivers were derived from the ottocoded hydrographic basin data (1:250000) from the Agência Nacional de Águas (ANA) available at http://www.snirh.gov.br/hidroweb.

Slope was the only variable in our models to test the effect of topography in WLP movements. The slope data was downloaded from TOPODATA website (http://www.webmapit.com.br/inpe/topodata/). This is one of the topographic data derived from Shuttle Radar Topographic Mission (SRTM) which is a radar system based on the interferometry technique that was used to create a Digital elevation model providing topographic information with a 30m resolution for the whole Brazilia territory (Valeriano and Rossetti, 2012).

All predictors (Figure 4) were rescaled or calculated with cell size set to 900 m^2 resolution and projected to the same projected coordinate system UTM zone 21S and datum WGS 84.

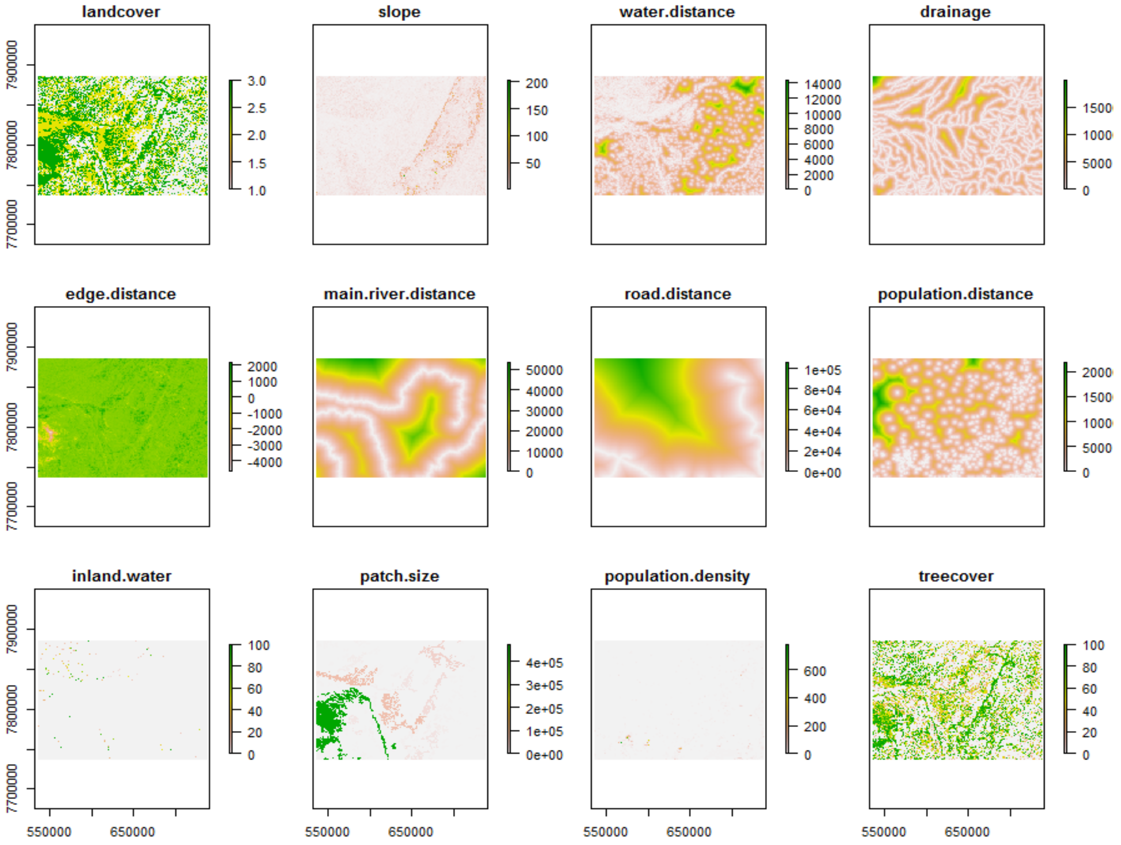

Figure 4. The twelve landscape variables tested in the Step Selection Analysis for white-lipped peccaries monitored with GPS collars in Mato Grosso do Sul state, Brazil.

2.6. Movement and Integrated Step Selection Function Analysis

To prepare data for movement analysis we have excluded the first two days of monitoring because we considered that in this interval WLP movements could be atypical since individuals were still returning from anesthesia procedures, re-joining their herds and adjusting for the collars recently deployed. We have also excluded the final days of monitoring when we detected a failure on the collar fix transmission and the intervals of data collection were irregular or inconsistent.

We used different measures to explore movement patterns of WLP. Step length (the distance between two consecutive fixes), turning angle distribution (relative angle measured step by step) and gap crossing capacity (permeability distance that can be reached by the animal in the matrix) were plotted and analyzed to compare movement patterns of different individuals and herds within each study site.

We have applied step selection functions (SSF) (see Fortin et al., 2005; Thurfjell et al., 2014) to test which landscape structure variables have effect on movement and habitat selection, only for the individuals that had at least one complete month of data transmitted and after regularizing fixes for 6 hour intervals (4 fixes per day) for all the individuals, and because of this filtering we did the step selection analysis for 24 individuals. The variables tested for this first model were: land cover (with 3 categories: forest, non-forest natural cover, matrix), patch size, percent tree cover, edge distance or distance from fragment center, distance from water source, distance from drainage, human density, distance from paved road and slope. We did a collinearity test to select for the variables that would be tested in the same models. As land cover, percent tree cover and edge distance showed Pearson correlation > 0.7 we opted to exclude land cover from the models (since not all individuals use all the land cover classes) and we tested tree cover and edge distance in separate models.

The step selection function is a new modeling approach that can be used to model habitat selection and movement together (Signer et al., 2019). SSF are based on Resource Selection Functions (RSF) that are defined as a statistical models used to estimate the relative probability of an individual selecting a resource when comparing the resources used by it (and covariates associated with GPS locations) versus the resources available in a determined area (Manly et al., 2002; Thurfjell et al., 2014), the selection occurs when a resource is used if it is encountered (Lele et al., 2013). In the SSF analysis, we use the steps decisions (i.e. segments of displacement) as the sampling units of the selected resources instead of using only the individual location (Fortin *et al*., 2005), which is the common procedure for RSF (Gillies et al., 2006).

In SSF the available resources are estimated using random alternative steps that could have been chosen by the individual, therefore we try to estimate accessible resources using alternative steps. By comparing each real step with the random steps we can estimate the strength of selection for the environmental covariates associated with the movement decision, so we incorporate a behavior decision interpretation on a habitat selection analysis (Thurfjell et al., 2014). Step selection functions are usually estimated by applying conditional logistic regressions, we use the model coefficients of the regression to evaluate if the covariates associated with the steps (our resources) had a positive (attraction) or negative effect (repulsion) on the step selection.

Although SSF has been extensively used (*e.g.* Beyer et al., 2016; Davies et al., 2017; Fortin et al., 2005; Panzacchi et al., 2016; Thurfjell et al., 2014) some challenges still exist to fit a more realistic model. For example, determining the available steps can be done by sampling the random steps from empirical distribution of the real steps (Avgar et al., 2016; Fortin et al., 2005) but we assume that habitat selection is conditional to movement decision, usually not quantifying the opposite, which is how movement capacity is affecting habitat selection (Avgar et al., 2016). This can lead to biased estimates of habitat selection, therefore a new approach named integrated step selection function (iSSF) was proposed integrating habitat selection and movement analysis in the same model, which is done by attributing analytical distributions for the available steps and including both habitat and movement data as covariates in the model (Avgar et al., 2016; Signer et al., 2019).

In our analysis we have used the amt package for R (Signer et al., 2019) which allow us to use maximum likelihood to fit gamma (Avgar et al., 2016; Signer et al., 2019) and Von Mises distributions (Duchesne et al., 2015; Signer et al., 2019) to the step length and turn angles data. Therefore we can generate the random steps and angles from this fitted distribution (Avgar et al., 2016; Signer et al., 2019). We used a two-step approach, first looking for each individual coefficient for all the landscape variables, and then deriving the final mean population coefficient of selection (β coefficients values).

Since iSSF can be treated as Poisson point-process model (Muff et al., 2018; Renner et al., 2015), with an approach recently proposed by Muff et al. (2018) we can use Bayesian and

Frequentist methods to fit step selection models accounting for random effects, which can be used to include inter-individual and herd variability in habitat selection. Generalized linear mixed effect models (Zuur et al., 2007; Zuur and Ieno, 2016) were applied accounting for the individuals and herds as random effects for the step selection analysis. We tested different models using the Akaike information criterion corrected values and the model weight to evaluate the proposed models.

3. RESULTS

3.1. General results

Field work was carried between July of 2013 and October of 2016, during this period we have captured 105 WLP from which 67 were females and 38 were males. Forty-five individuals were captured in the Cerrado region and sixty were captured in Pantanal. Fifty-four individuals were classified as adults by age class and weight. From this, thirty white-lipped peccaries received GPS collars (Table 1), 18 females and 12 males, and we have managed to retrieve 28,186 fixes from those individuals. The time of GPS monitoring for each individual varied between 1 (31 days) to 12 months (371). Twenty four individuals were selected for the Step Selection Analysis because we could regularize their fixes for a 6h interval - 4 fixes per day (see individuals featured in grey at Table 1).

Table 1. Adult white-lipped peccaries monitored with GPS collars between 2013 and 2016 in the Cerrado highlands and Pantanal wetlands of Mato Grosso do Sul state. We present data about the study area, sex, the period of monitoring and the number of fixes successfully acquired with satellite transmission for all individuals. Individuals featured in grey were selected for the step selection analysis.

Individual	**Biome**	**Area/Herd**	**Sex**	**Start transmission**	**Finish transmission**	**Fixes/ day**	**Total days**	**Total fixes**
Bruna	Pantanal	Caiman 2	F	14-Aug-15	4-Aug-16	8	356	**2797**
Canela	Pantanal	Barranco Alto	F	28-Jun-15	23-Nov-15	8	148	**1165**
Cida	Cerrado	Safira	F	18-Dec-15	5-Oct-16	8	292	**1293**
Claudio	Pantanal	23 de Marco	M	30-Aug-14	14-Nov-14	4	76	**275**
Cleide	Cerrado	Jacobina	F	9-Mar-15	23-Nov-15	8	259	**1760**
Dan	Cerrado	Colorado	M	22-Jun-16	26-Oct-16	8	126	**73**
Ge	Pantanal	Barranco Alto	M	27-Jun-16	16-Dec-16	8 and 6	172	**908**
Jay	Cerrado	Colorado	M	11-Jul-13	28-Oct-13	4	109	**380**
Joao Paulo	Cerrado	Colorado	M	21-Feb-15	30-Mar-15	24 and 12	37	**310**

Julia	Cerrado	Claudia	F	28-Jul-14	6-Dec-14	4	131	**349**
Lili	Pantanal	Caiman 1	F	3-Dec-14	3-Jan-15	4	31	**113**
Lucas	Pantanal	Barranco Alto	M	1-Jun-15	27-Jul-15	8	56	**457**
Lurdes	Cerrado	Colorado	F	5-Jun-14	17-Jan-15	4	226	**462**
Malu	Cerrado	Safira	F	8-Jun-14	11-Dec-14	4	186	**504**
Malu II	Cerrado	Safira	F	30-Sep-15	7-Mar-16	8	159	**733**
Marcello	Pantanal	Caiman 1	M	15-Aug-15	5-Mar-16	8	203	**1246**
Marcos	Cerrado	Taboco	M	18-Feb-16	29-Apr-16	8	71	**40**
Mario	Pantanal	Caiman 2	M	14-Aug-15	17-Mar-16	8	216	**990**
Nalva	Cerrado	Claudia	F	27-Jul-14	2-Sep-14	4	37	**60**
Nanda	Pantanal	Barranco Alto	F	24-Jun-15	13-Jan-16	8	203	**1584**
Norma	Pantanal	23 de Marco	F	31-Aug-14	1-Feb-15	4	154	**507**
Pumba	Pantanal	23 de Marco	F	20-Apr-15	4-Jan-16	8	259	**1800**
Roberta	Pantanal	Caiman 1	F	16-Aug-15	21-Aug-16	8	371	**2935**
Rosana	Pantanal	23 de Marco	F	24-Nov-15	21-Jul-16	8	240	**1240**
Simao	Pantanal	23 de Marco	M	20-Apr-15	8-Jul-15	8	79	**138**
Tainara	Cerrado	Jacobina	F	9-Mar-15	20-Jan-16	8 and 6	317	**1644**
Tereza	Cerrado	Santa Tereza	F	6-Mar-15	24-May-15	4	79	**110**
Toninho	Cerrado	Safira	M	8-Jun-14	25-Nov-14	4	170	**397**
Trina	Pantanal	Barranco Alto	F	26-Jun-15	3-Mar-16	8	251	**1598**
Vagner	Cerrado	Taboco	M	18-Feb-16	11-Aug-16	8	175	**1151**
Valentina	Cerrado	Santa Tereza	F	9-Aug-15	7-Mar-16	8	211	**1167**

We have analyzed turning angles (Figure 5) and step length distributions (Figure 6) for all the twenty-four individuals after regularizing the fix rates to 4 fixes per day for each one of them. Most step lengths for 6 hour intervals were concentrated in distances between 0 and 2000m. We can see that there was individual variation in turning angles distribution, with some individuals presenting more straight directions in some periods of the track, but most data evidencing homogeneity in the distribution of angles what indicates a more restricted space use, which indicates a home range behavior for most WLP monitored.

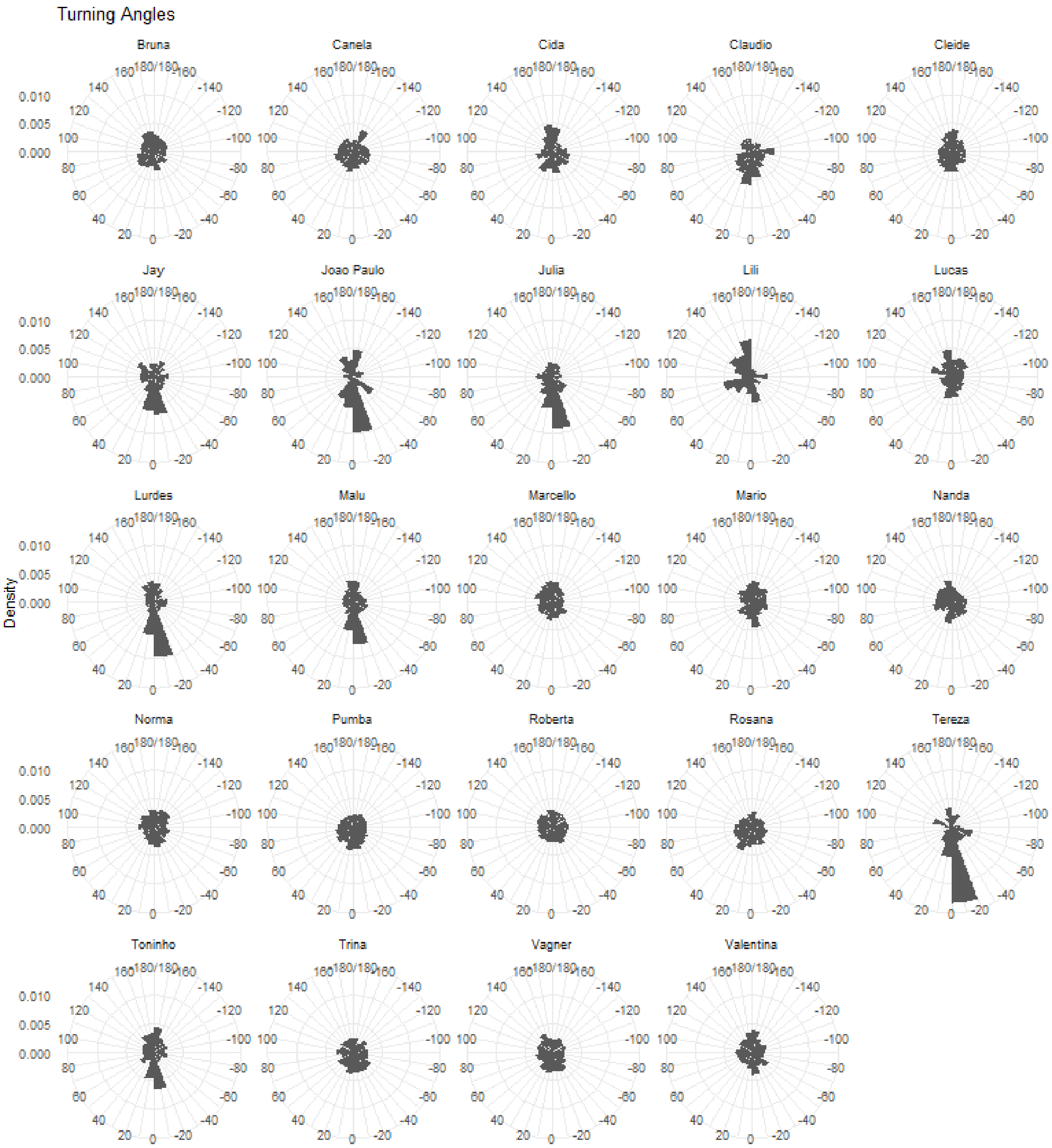

Figure 5. Turning angles distribution for twenty-four white-lipped peccaries monitored with GPS collars in Mato Grosso do Sul state, with fix rate regularized for 6 hour interval.

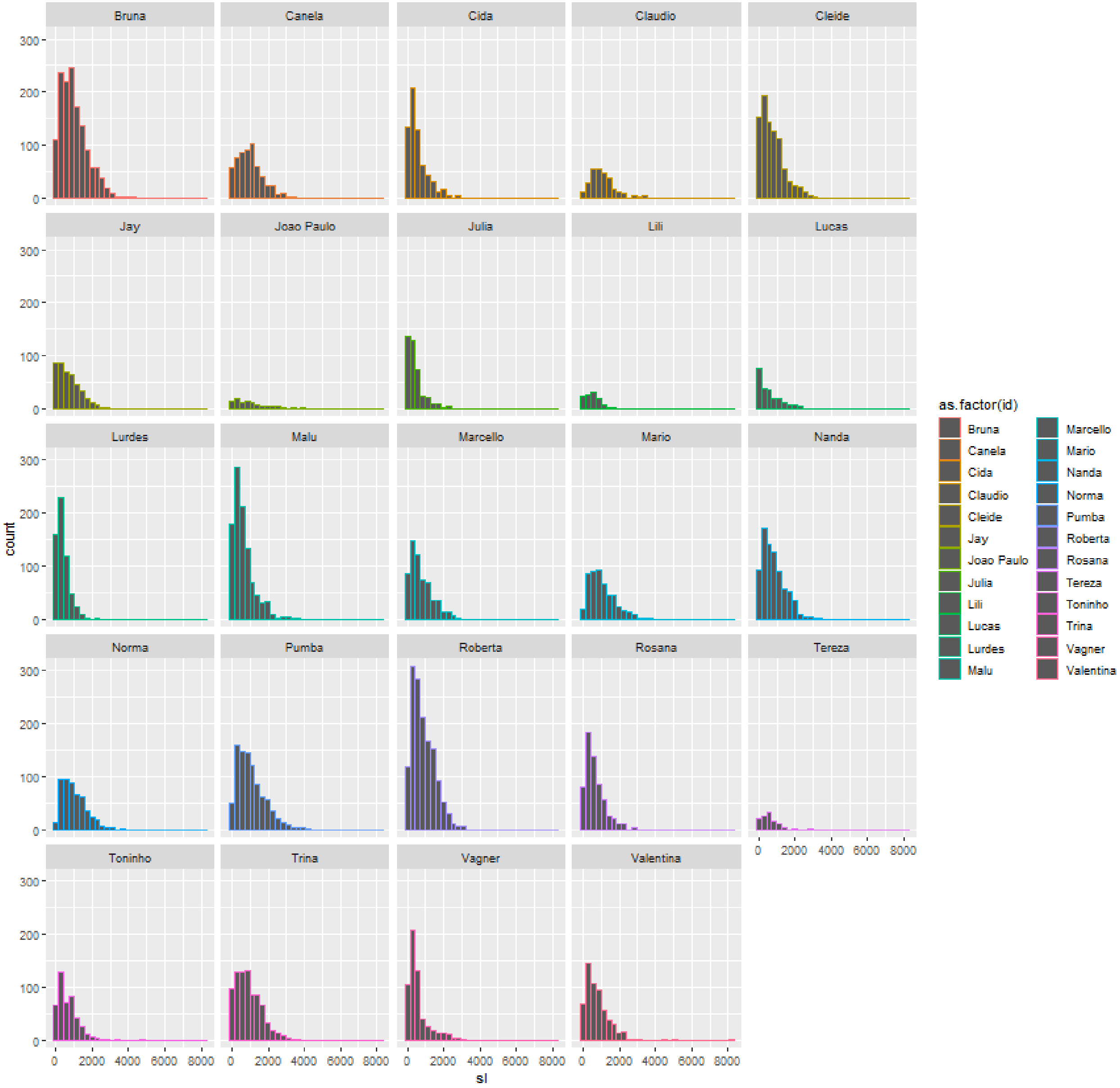

Figure 6. Step length distribution for twenty-four white-lipped peccaries monitored with GPS collars in Mato Grosso do Sul state, with fix rate regularized for 6 hour interval.

3.2. Gap crossing capacity

We have analyzed the distances that individuals were capable to permeate in the matrix (mainly pasture for cattle ranching in our study sites), and in the two other land cover classes: natural non-forest vegetation and forest. In the matrix, WLPs presented different levels of sensitivity for gap crossing capacity. Five individuals (Cláudio, Norma, Pumba, Lucas, and João Paulo) avoided pasture areas and did not use the matrix (TRUE case positions in Figure 7); although the distribution of the random step (FALSE case positions in Figure 7) showed that there was pasture available in reachable distances for them. Most individuals used distances between 0 and 200m in the matrix, with peaks between 0 and 100m, and the maximum distance achieved by them was 697.2 meters (Figure 7). In natural-non forest vegetation distances, WLP used areas concentrated between 0 and 100m (Supplementary material). And in the forest areas, WLP used all the available extension of forest mostly concentrated between 0 and 250m, with proportional distribution of use/availability (Supplementary material).

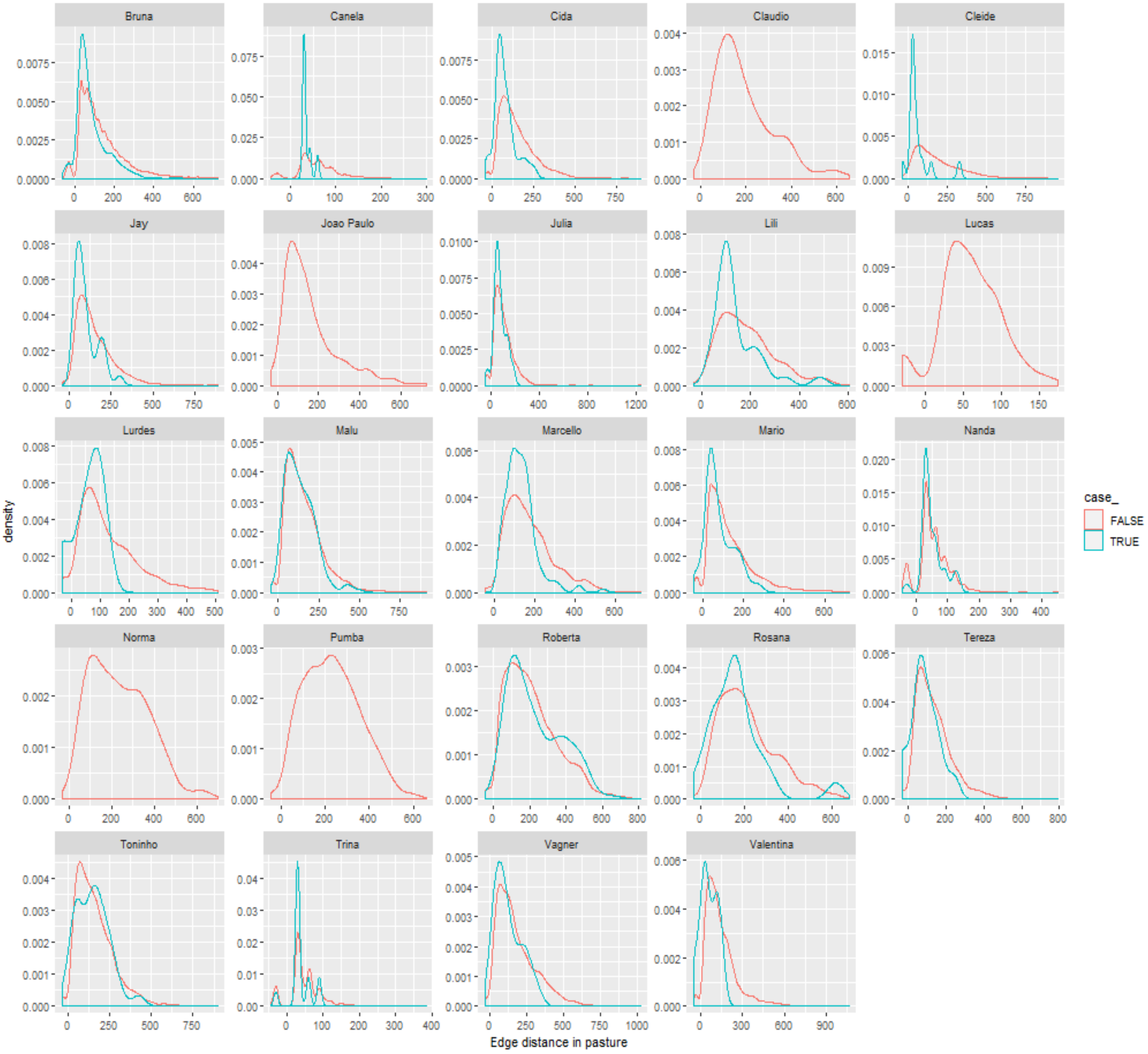

Figure 7. Edge distance in pasture matrix for used (TRUE case) and available steps (FALSE case) of twenty-four white-lipped peccaries monitored with GPS collars in Mato Grosso do Sul state. Edge distance was calculated with Euclidean distance

3.3. Paved road distance

Distance from paved roads, one of the variables tested in our Step Selection Analysis, was one component of the landscape that we hypothesize that could work as a barrier for

WLP. We have plotted and analyzed the distribution of steps and associated paved road distances (Supplementary material). In Pantanal individuals reached areas 5937m distant, and that was the closest distance from roads. In the Cerrado, the minimum distance from paved roads associated with WLP steps was 0 m. However, accounting for the pixel resolution of 30m, individuals could have used areas distant from 0 to 30m of paved roads. To check if individuals had crossed the existent paved roads, we have plotted the locations of herds living close to the roads. Maps showed that WLPs living in close proximity with paved roads did not cross them (Figure 8) in the period that they were monitored, from June of 2014 to October of 2016.

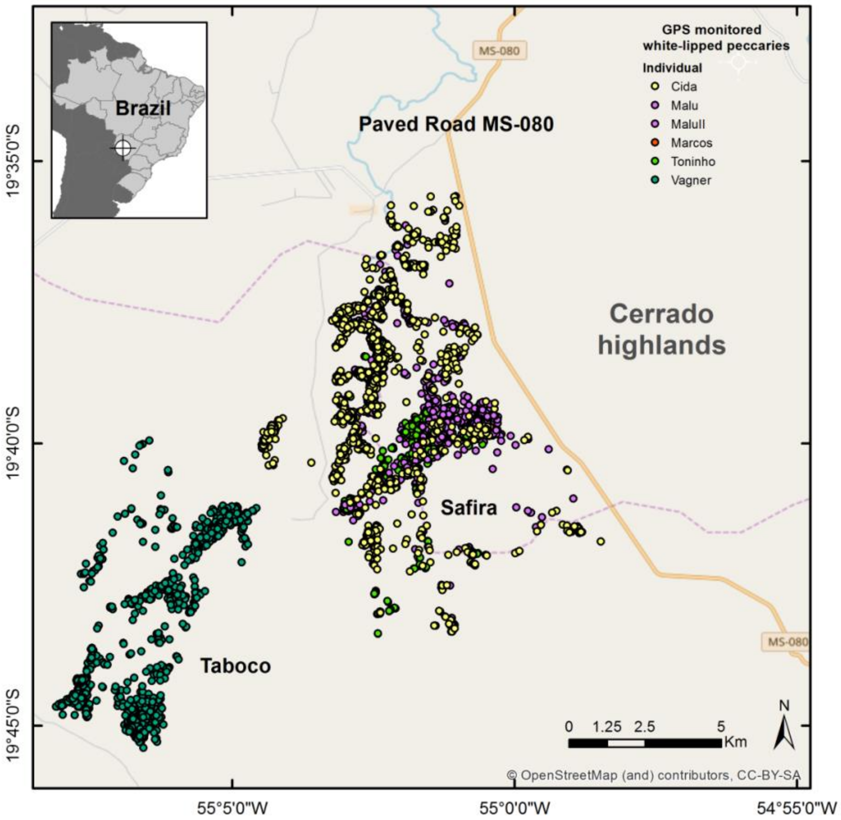

Figure 8. Safira and Taboco herds, identified by white-lipped peccaries GPS locations in the Cerrado highlands in the municipality of Corguinho. Individuals from the Safira herd did not cross the paved road (MS-080) while we monitored the herd between

3.4. SSF - Two-step approach results

Coefficients interpretation in a SSF analysis reflect habitat selection in a more local spatial and temporal scale than in regular RSF, and that is why it is possible to relate movement decisions with habitat characteristics in such analysis. Each coefficient can be interpreted as the isolated effect of the tested variable, keeping the other variables tested in the model with constant. Therefore, the strength of selection for each variable represents the relative chance of the individual choosing a location as a function of its spatial characteristics.

Our results showed a positive selection of WLP for natural vegetation and forest areas when compared with the matrix (Supplementary material). Since not all individuals used the three cover classes tested, we excluded the categorical variable (landcover) from the population analysis and kept only the continuous variables in the tested models.

A higher percent of tree cover, larger forest patches, proximity to water sources and proximity with fragment center had a positive effect on habitat selection. WLP avoided steep slope areas, paved roads, and areas of higher population density. In our two-step approach, we first looked for each individual model with all the landscape variables and then we derived the final mean population coefficient of selection (β coefficients values). The individual plots for each variable tested show the values associated with each individual selection estimate.

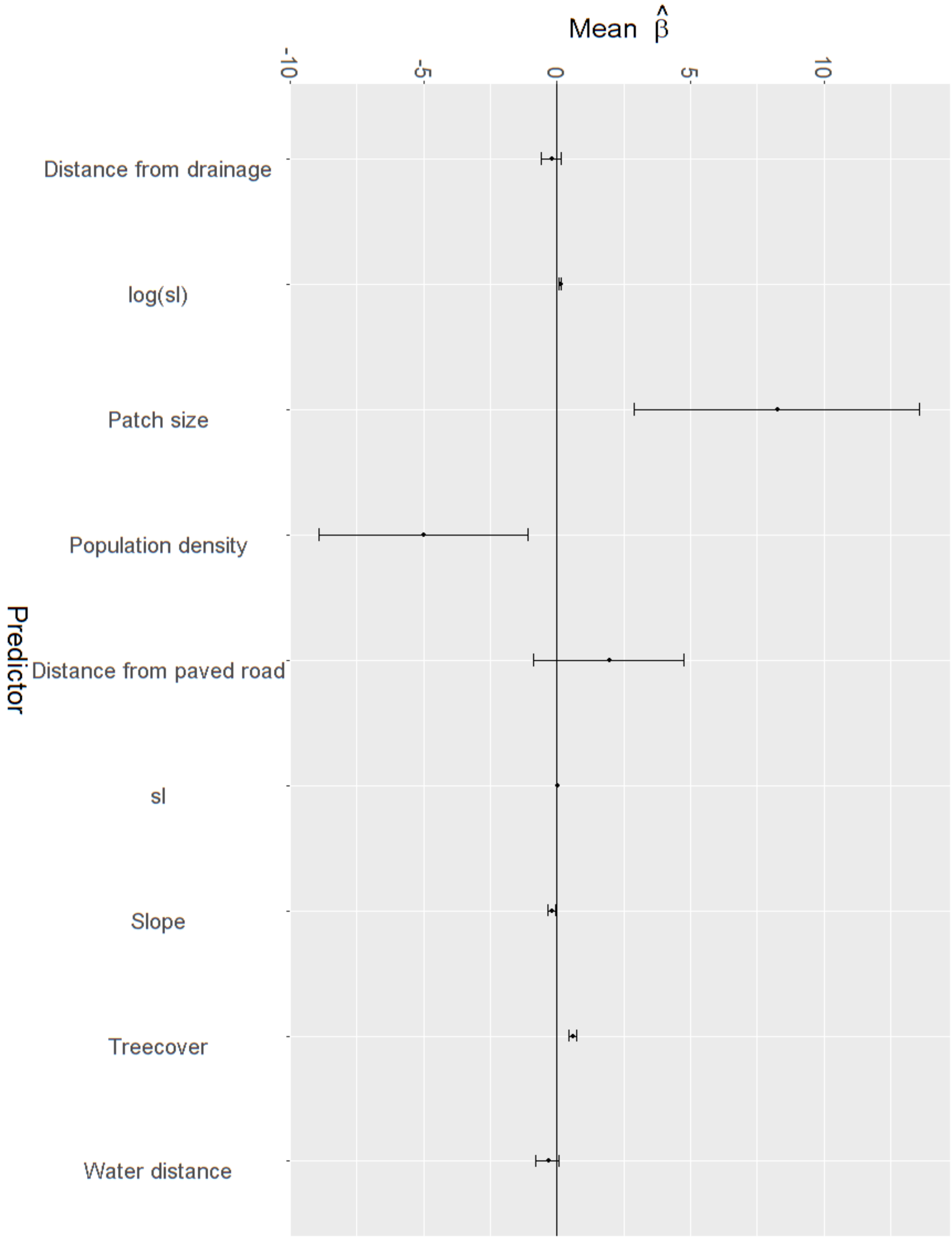

Figure 9. Model 1 estimate results for SSF analysis with the two-step approach. We have analyzed adult white-lipped peccaries movement and habitat selection between 2013 and 2016 in the Cerrado highlands and Pantanal wetlands of Mato Grosso do Sul state. Dots show the results for estimated coefficients of the twenty-four individual conditional logistic regression models.

Table 2. Two-step approach results for SSF analysis. We have analyzed adult WLP movement and habitat selection between 2013 and 2016 in the Cerrado highlands and Pantanal wetlands of Mato Grosso do Sul state. The population coefficients show the mean of the β coefficients and standard deviation for β coefficients values for all twenty-four individual models.

Two Step Approach Results

Model 1

```
mod1 <- clogit(case_ ~
treecover.sc+patch.size.sc+slope.sc+drainage.
sc+population.density.sc+road.distance.sc+wa
ter.distance.sc+sl+log(sl)+ strata(step_id),
data = data)
```

pop.coef

term	mean beta	se mean beta
drainage distance	-0.218	0.188
log(sl)	0.102	0.017
patch size	7.720	2.570
population density	-4.130	1.460
road distance	1.910	1.580
sl	0.000	0.000
slope	-0.192	0.071
treecover	0.576	0.079
water distance	-0.359	0.220

Model 2

```
mod2 <- clogit(case_ ~
edge.distance.sc+patch.size.sc+slope.sc+drain
age.sc+population.density.sc+road.distance.sc
+water.distance.sc+sl+log(sl)+ strata(step_id),
data = data)
```

pop.coef2

term	mean beta	se mean beta
drainage	-0.285	0.204
edge.distance	-0.565	0.088
log(sl)	0.104	0.016
pacth size	6.870	2.640
population.density	-4.130	1.470
road.distance	1.450	1.540
sl	0.000	0.000
slope	-0.105	0.059
water distance	-0.309	0.193

3.5. SSF - Random Effect Results

Random effect model results showed the same patterns of selection acquired with the two-step selection approach. Although the strength of selection had different variables being more significant if we accounted for individual or herd variation. For the models accounting for individual variation, the variables of percent of tree cover, forest patch size, slope, population distance, and inland water frequency were the most important variables driving habitat selection for WLP. Individual variability in selection response was higher for patch size, road distance and inland water variables (Table 3). For the models accounting for herd variation, the variables of percent of tree cover and inland water frequency were the most important variables driving habitat selection for WLP. Herd variability in selection response was higher for the road distance and patch size variables (Table 4).

Table 3. Random effect model results for SSF analysis accounting for individual variation. We have analyzed adult WLP movement and habitat selection between 2013 and 2016 in the Cerrado highlands and Pantanal wetlands of Mato Grosso do Sul state. The β coefficients show values for the generalized mixed effect model with a Poisson distribution fitted for all twenty-four individuals and using individual variation as a random effect.

Random Effect Models accounting for individual variation
Best model 1

```
TMBStruc = glmmTMB(Loc ~
treecover.sc+patch.size.sc+slope.sc+drainage.sc+population.distance.sc+road.distance.sc
+water.distance.sc
+inland.water.sc+(1|step_id) +
(0 + treecover.sc | ANIMAL_ID) + (0 + patch.size.sc | ANIMAL_ID) +
(0 + slope.sc | ANIMAL_ID) +
(0 + drainage.sc | ANIMAL_ID)
+
(0 + population.distance.sc | ANIMAL_ID) +
(0 + road.distance.sc | ANIMAL_ID) +
(0 + water.distance.sc | ANIMAL_ID)+
(0 + inland.water.sc | ANIMAL_ID), family=poisson, data=ssfdat, doFit=FALSE)
```

Family: poisson (log)

AIC	BIC	logLik	deviance	df.resid

136363.5	136544.2	-68164.8	136329.5	305449	
Random effects:					
Conditional model:					
Groups	**Name**	**Variance**	**Std.Dev.**		
step_id	(Intercept)	1.00E+06	1000		
ANIMAL_ID	treecover.sc	5.13E-02	0.2264		
ANIMAL_ID.1	patch.size.sc	3.97E+01	6.2971		
ANIMAL_ID.2	slope.sc	6.27E-02	0.2504		
ANIMAL_ID.3	drainage.sc	5.02E-01	0.7083		
ANIMAL_ID.4	population.distance.sc	7.50E-01	0.8658		
ANIMAL_ID.5	road.distance.sc	7.85E+00	2.8018		
ANIMAL_ID.6	water.distance.sc	1.76E-01	0.4191		
ANIMAL_ID.7	inland.water.sc	2.05E+02	14.3056		
Number of obs:	305466,	groups:	step_id, 1442;	ANIMAL_ID, 24	
Conditional model:					
Estimate	**Std.**	**Error**	**z**	**value**	**Pr(>|z|)**
(Intercept)	-4.00823	26.33409	-0.152	0.87902	
treecover.sc	0.48744	0.04908	9.931	<2E-16	***
patch.size.sc	3.38483	1.39699	2.423	0.01539	*
slope.sc	-0.13408	0.05797	-2.313	0.02072	*
drainage.sc	0.15375	0.14932	1.03	0.30317	
population.distance.sc	-0.54621	0.18477	-2.956	0.00311	**
road.distance.sc	0.4741	0.66604	0.712	0.47657	
water.distance.sc	-0.16185	0.09918	-1.632	0.10269	
inland.water.sc	-8.38763	3.30911	-2.535	0.01125	*

Table 4. Random effect model results for SSF analysis accounting for herd variation. We have analyzed adult WLP movement and habitat selection between 2013 and 2016 in the Cerrado highlands and Pantanal wetlands of Mato Grosso do Sul state. The β coefficients show values for the generalized mixed effect model with a Poisson distribution fitted for all twenty-four individuals and using herd variation as a random effect. We have monitored 10 herds from which 6 were from the Cerrado area and 4 from the Pantanal area.

Random Effect Models accounting for herd variation

Best model

```
TMBStruc.herd1 =
glmmTMB(Loc ~
treecover.sc+patch.size.sc+
slope.sc+drainage.sc+population.
density.sc+road.distance.sc
+water.distance.sc+
inland.water.sc+(1|step_id)+
(0 + treecover.sc | HERD_ID) +
(0 + patch.size.sc | HERD_ID) +
(0 + slope.sc | HERD_ID) +
(0 + drainage.sc | HERD_ID) +
(0 + population.density.sc |
HERD_ID) +
(0 + road.distance.sc | HERD_ID)
+
(0 + water.distance.sc |
HERD_ID), family=poisson,
data=ssfdat, doFit=FALSE)
```

Family: poisson(log)

AIC	BIC	logLik	deviance	df.resid
136745.6	136915.6	-68356.8	136713.6	305450

Random effects:

Conditional model:

Groups	**Name**	**Variance**	**Std.Dev.**
step_id	(Intercept)	1.00E+06	1000
HERD_ID	treecover.sc	4.88E-02	0.221
HERD_ID.1	patch.size.sc	6.77E+00	2.6025
HERD_ID.2	slope.sc	8.72E-02	0.2952
HERD_ID.3	drainage.sc	9.17E-02	0.3027
HERD_ID.4	population.density.sc	1.26E-02	0.1122
HERD_ID.5	road.distance.sc	7.85E-01	0.8861
HERD_ID.6	water.distance.sc	3.10E-01	0.5563

Number of obs: 305466, groups: step_id, 1442; HERD_ID, 10

Conditional model:

Estimate	**Std.**	**Error**	**z**	**value**	**Pr(>|z|)**
(Intercept)	-3.70179	26.33412	-0.141	0.888	
treecover.sc	0.53042	0.07123	7.446	9.60E-14	***
patch.size.sc	0.69471	0.87538	0.794	0.427	
slope.sc	-0.10887	0.09652	-1.128	0.259	

drainage.sc	-0.11416	0.09911	-1.152	0.249	
population.density.sc	-0.09823	0.07367	-1.333	0.182	
road.distance.sc	-0.29854	0.30854	-0.968	0.333	
water.distance.sc	-0.21852	0.1802	-1.213	0.225	
inland.water.sc	-0.19673	0.01937	-10.155	< 2E-16	***

4. DISCUSSION

The WLP use large and ecologically diverse areas through its distribution, and it is an important keystone species in Neotropical forests (Altrichter et al., 2012; Jorge et al., 2013; Keuroghlian et al., 2009) but still little is known about the species fine-scale movement patterns and habitat selection. The WLP populations in the Cerrado and Pantanal of Brazil are currently highly susceptible to human impacts mainly due to land cover modifications, fragmentation, and hunting (Ferreira et al., 2017; Jácomo et al., 2013; Jorge et al., 2019; Keuroghlian et al., 2013). We have explored how WLP movement decisions are affected by the landscape structure and human impacts in the UPRB to support new conservation strategies that could be implemented regionally and protect WLP populations' persistence. Our results based on the tracking and monitoring of 24 individuals from 10 herds showed that individuals can respond differently to the same landscape variables, but that general population patterns indicate the importance of well-preserved forest patches and riparian environments to guarantee connectivity for WLP in our study region.

In recent years, the landscape in UPRB has been modified by the expansion of cattle ranching, with consequent habitat loss and fragmentation which affect WLP populations directly, through habitat modification, and indirectly because WLPs can search for low-cattle impacted regions depending on resource availability (Eaton et al., 2017). Deforestation in the UPRB changes the landscape structure in both the plain and in the plateau of the river basin, but the Pantanal has additional changes since the forest loss in the plateau increases the erosion rates, and accelerate the river avulsions in the Pantanal. Consequently, the native vegetation will also change in the areas affected by the avulsions (Assine, 2005; Roque et al., 2016). The Pantanal is a very dynamic environment and integrating river and landscape dynamic data into ecological models to test WLP movement responses is important to predict possible future scenarios for the species persistence and distribution through the UPRB. Our SSF results have indicated that a higher percent of tree cover, larger forest patches, proximity to water sources and proximity with fragment center had an attraction effect for WLP movement decisions and habitat selection; therefore these variables are indicators of important resources. However, proximity to paved roads and to areas of higher population density had a negative effect, repelling WLP what can indicate a behavior response of avoidance and the possible creation of barriers. Areas of steep slopes were also avoided by WLP.

4.1. Gap crossing capacity

With our SSF results for gap crossing analysis, we were able to determine the distances that WLPs were traversing in the matrix. We identified individual variation in the movement response to the forest edge distance, with some WLPs crossing matrix areas while others avoided pasture areas. We observed that the local context in which the herd is living in is determinant for the individuals' behavior response. With exception of individuals from the Caiman 1, Caiman 2 and Barranco Alto herds, which are farms that mainly foment wildlife observation tourism, we have noticed that WLP have a shy behaviour towards human presence in the Fazendas (farms). The avoidance behavior could be related to two main factors: the presence of domestic dogs and/or illegal hunting in the Fazendas surroundings. We have observed that the local farms main economic activity and their management system (allowing dogs or not, restricting the areas that tourists can visit and the activities that can display) can influence the WLPs movement behavior, which is also observed for other species, such as the jaguars (*Panthera onca*). In the Cerrado, we have found wildlife illegal hunting evidence in different areas, and also in some Fazendas surroundings in the Pantanal, illegal hunting evidence were also documented during our field work activities.

Most individuals displayed matrix cross distances between 0 and 200m, and the maximum distance reached by them was 697 meters. In natural-non forest vegetation cover, the WLP movements were concentrated between 0 and 100m (Supplementary material). This information is essential to design functional corridors for WLPs since the capacity to cross open areas is directly associated with the species potential to maintain sustainable populations (Ribeiro, 2010). The gap crossing capacity brings consequences for gene flow across the landscape because it will restrict or allow individuals to reach different forest patches (Doherty and Driscoll, 2018; Fahrig, 2017).

The distance from the edge of the fragment was used to estimate the gap crossing capacity for WLPs in our study region but it was also used to verify if we could detect some edge effect on WLP movement decisions. In the forest areas, WLP used all the available extension of the forest, mostly concentrated between 0 and 250m. Since the use/availability proportion for the forest extension was very similar for most WLPs (Supplementary material), indicating that they explore all the forest extension available for them, we did not verify avoidance for regions near the fragment boundaries. In fact, we have shown that the vicinity of the forest boundaries was an important region for WLP because it was where the matrix and non-forest native vegetation covers were mostly explored. When foraging or traveling in open habitats such as pasture and grasslands, the proximity to the forest fragment edges gives WLP a closer escape route to return to more “protected” forest habitats. Such behavior to move along the forest fragment edges was already described for WLPs in the Brazilian Pantanal (Eaton et al., 2017; Keuroghlian et al., 2015) and also for the wild boar (*Sus scrofa)* in Sweden (Thurfjell et al., 2014, 2009).

4.2. Paved roads acting as barriers for white-lipped peccaries

The proximity to paved roads and to areas of higher population density had a negative effect on WLP movement decisions and habitat selection. Paved roads and high altitude plateaus which are accessible only through steep slope terrains have functioned as barriers for WLPs from, respectively, the Safira and Jacobina herds that were monitored in the Cerrado. Although, we have verified that WLPs do cross dirt roads, mainly in regions where forest fragments are close to the road in both roadsides, for example for the Santa Tereza herd. The proximity to roads was also an important variable affecting WLP distribution in the Atlantic Forest (Jorge et al., 2013). Areas with higher human population density and near paved roads, which provide easier human population accessibility, can increase hunting and other human-wildlife conflicts for WLP in forest fragments near them (Trombulak and Frissell, 2000).

We have also hypothesized that WLP could be avoiding the paved roads crossing because we did not register any WLP road kill during our field work. In a recent publication, with more than 21,000 records of wildlife road kill in Brazil, the authors did not register even one single road kill for WLPs (Grilo et al., 2018) which indicates that the species can be really avoiding paved road crossing. As it was highlighted by Shepard et al. (2008), the genetic effects of roads acting as barriers in populations of long-lived species may not be detected over short time-scales, what would delay effective management actions to revert the problem. Besides, the genetic diversity in WLP populations from the Cerrado, Pantanal and Atlantic forest was affected by the geographical distance among them, and dispersal events showed to be limited to distances up to 180km (de Góes Maciel et al., 2019). Therefore to avoid populations' isolation and improve connectivity for WLP in future conservation management projects, we should consider paved roads, areas with a high density of human population, areas with steep slopes and dispersal distance among WLP populations as possible barriers for the species.

4.3. Individual and herd variation as random effects

Finally, our analyses have shown that the strength of selection had different variables being more significant if we accounted for individual or herd as random effect in the glmm models. The landscape context in which each herd is living and the periods in which each individual was monitored certainly influenced this variability in movement and habitat selection response. Individual and herd variability in selection response was higher for patch size and road distance variables. The areas used by the different individuals have different resource distribution and landscape features available. Therefore, if we consider the individual movement capacity and the landscape characteristics available for each herd, we will detect that a different range of forest fragment sizes were selected by them, as well as different distances from roads and water sources.

In sum, we have shown that movements and habitat selection of WLPs in the UPRB can have individual and herd variation, and that could be affected by the landscape context in which each herd is currently living. In a long term, those individual variations could be important to maintain the genetic diversity among populations considering that the individuals' gap crossing capacities and the dispersal abilities will play an important role in determining the patterns of habitat use in heterogeneous altered landscapes (Fahrig, 2007). The human impacts in the Pantanal and Cerrado of the UPRB are creating barriers that should be considered in ecological corridor planning for the species. The general patterns of habitat selection for WLP identified in our study corroborate what previous studies have shown, the WLPs depend on forest habitats and areas near watercourses to live (Fragoso, 1998; Hofman et al., 2018; Jorge et al., 2019; Keuroghlian and Eaton, 2008a; Reyna-Hurtado et al., 2016) therefore reinforcing the importance of Brazilian laws to protect riparian habitats e maintaining functional connected forest areas will be essential for the species persistence in the UPRB, since the recent evaluations predict that if the current deforestation rates continue as they are in the UPRB, the native vegetation is predicted to be loss by 2029 in the plateau and by 2045 in the plain (Roque et al., 2016; Silva et al., 2011). Implementing effective actions to promote habitat protection and policy changes is an urgent requirement for the

WLP conservation through all its distribution (Altrichter et al., 2012). We expect that our results provide a better comprehension of the WLP movement and habitat selection responses to the local landscape and human impacts, to support conservation managers' decisions in the UPRB.

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IV CHAPTER 3

Can movement patterns, home range and displacement rates be used as indicators of habitat quality for the last large-herd-living ungulate of neotropical forests?

ABSTRACT

The spatial-temporal changes that animals display in their movements and home ranges are made to optimize gains in fitness and to avoid the costs imposed by a constantly changing world. In this study, our aim was to explore the movements and home ranges of white-lipped peccaries (WLP - *Tayassu pecari*) living in heterogeneous productive landscapes of two Neotropical biomes, the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil. Thirty WLP individuals were monitored with GPS collars between 2013 and 2016 so that we could evaluate: (1) Are individuals from different biomes displaying similar patterns of movement and home range? (2) Can we detect differences in the movement patterns of male and female WLPs? (3) Can we detect different movement modes and average distance traveled per day in the different seasons and regions of study? (4) How landscape structure and habitat quality is influencing the herds' space use patterns? We have analyzed 3 movement metrics (daily displacement, median speed and net square displacement - NSD) and 3 methods to estimate evaluate home range size: minimum convex polygon (MCP), kernel density estimator with the minimum reference bandwidth (minHREFK) and the autocorrelated kernel density estimator (AKDE). The mean daily distance for the monitored individuals was 3501m and median speed 0.03m/s. The average distance moved per day and the average median speeds were higher for the individuals monitored in the Pantanal than for the individuals monitored in the Cerrado. In contrast, average home range size and the average NSD were higher for the individuals in the Cerrado than for the individuals in the Pantanal. The total home range size had mean values varying depending on the estimator used: 28 km^2 (MCP), 33 km^2 (minHREFK) and 52 km^2 (AKDE). Monthly home range size had average of 26 km^2 (minHREFK) and the mean NSD analysis applied for monthly data showed that, although WLP usually display a home range behavior when we look for the entire trajectory of each individual, the movement mode can change among different months, and in this scale of time (30 days) we can identify nomadic and dispersal behaviors. With this study, we could identify that seasonal changes in resources and the landscape context can trigger changes in the home range behavior during the animals' lifetime. Analyzing movement and home range behavior of individuals in different biomes and scales of time and space can drive different conclusion about the habitat requirements for the species persistence and that information is essential for the species conservation in heterogeneous productive landscapes.

Keywords: Tayassu, kernel, net square displacement, habitat selection, fragmentation.

1. INTRODUCTION

Movement of organisms is determined by behavior responses to internal and external drivers (Nathan et al., 2008). Therefore, movement behavior reflects the individual's adjustments in response to environmental changes that are constantly occurring in a dynamic changing world. Animals can adjust their space use depending on the resource availability, anthropogenic impacts, predator pressure and landscape modifications (Doherty and Driscoll, 2018; Fahrig, 2007; Nathan et al., 2008). The spatial-temporal changes that animals display in their movements are made to optimize gains in fitness and to avoid the costs imposed by the new obstacles that are eventually created with environmental changes (Fahrig, 2007).

In productive landscapes, different obstacles can be created for animals depending on the main economic activity that is being developed. The production landscapes are composed by mosaics of habitat and matrix with low to high complexity, which will demand different adjustments for species persistence locally. It can be expected that some animals would have to spend more time and energy moving to fulfill their daily resource requirements in modified landscapes than in pristine areas (Doherty and Driscoll, 2018). Contrarily, animal movement rates could also decrease in response to barriers and resource change driven by anthropogenic effects associated with landscape modifications (Tucker et al., 2018). But predicting the effects that modifications in the landscape can have on the movement patterns of animals is not a simple task. There is a myriad of factors that shapes habitat quality and landscape structure, which will influence the desire to move (internal state) and affect mobility and navigation capacities for different species in different ways (Doherty and Driscoll, 2018; Nathan et al., 2008).

In fact, landscape structure itself could be responsible to determine, in modified landscapes, what is a habitat of greater or smaller quality. Fragmentation and land cover change in production landscapes can create new habitats and the animals' responses will depend on their motion capacity, navigation capacity and also on their previous experience on altered landscapes and memory response (Doherty and Driscoll, 2018; Mueller and Fagan, 2008; Nathan et al., 2008). Animals that are less mobile may stay for long periods of time in the same fragment if there is enough resource available for them, searching for habitats with higher quality in different parts of a single patch (Doherty and Driscoll, 2018). For animals with long range movement capacity, and that depend on forest areas to live, habitat quality may influence their decision to stay or to move for a different forest patch, and landscape structure factors will then influence which are the new patches available for use and what are the costs (due to risks associated with matrix crossing) to reach those new patches (Doherty and Driscoll, 2018; Fahrig, 2007).

Animals can display different space use behaviours, which can be also defined as population-level distribution strategies (Mueller and Fagan, 2008). When individuals display residency patterns staying in a fixed home range, it may indicate that they find sufficient resources to stay in a defined range throughout the year, but animals can have also a nomadic or migratory behavior. Migration is represented by regular and seasonal use of two distinct areas that are separated by long-distance movement, forming spatially disjunct seasonal ranges (Mueller and Fagan, 2008). Nomadism behavior is more complex to define but it occurs when animals are not resident or migratory, and they display wandering movements with a lack of predictability of spatial or temporal patterns, and which usually can indicate that animals are searching for resources with an irregular and fluctuating distribution (Mueller and Fagan, 2008).

As a consequence of movement decisions in productive landscapes, the home range area used can also be affected by changes in the landscape structure and habitat quality. A home range is the area used for an animal in its daily activities (Burt, 1943; Powell and Mitchell, 2012), and having a defined home range is a consequence of the animals' decisions about restricting the space use to survive and reproduce in a specific area (Börger et al., 2008; Powell and Mitchell, 2012). Although there are different definitions for the concept of home range, this space use behavior can be interpreted as a product of decisions made by the animals to optimize the use of the resources that they need in the environments where they live, and that could help researchers to interpret and predict their cognitive maps (Börger et al., 2008; Powell, 2000; Powell and Mitchell, 2012). Seasonal changes in resources, modifications in the landscape and aging are examples of external and internal drivers that can trigger changes in the home range behavior during the animals' lifetime. Therefore, the home range from a single individual is also dynamic and can be measured in different time scales (Börger et al., 2008).

In this study, our aim was to explore movement and home range of white-lipped peccaries (WLP - *Tayassu pecari*, Link, 1795) living in heterogeneous productive landscapes of two Neotropical biomes, the Cerrado and Pantanal of Brazil. This frugivore-omnivore social ungulate species was chosen to be our model species because there is a lack of fine resolution movement information for the species. WLPs form the largest biomass of mammals in the forests where it lives (Beck, 2006; Eisenberg, 1980; Peres, 1996) and has an important role as ecosystem engineer, as prey for large carnivores and as seed predator and disperser in Neotropical ecosystems (e.g. Beck et al., 2010; Keuroghlian and Eaton, 2008a; Kiltie and Terborgh, 1983; Perilli et al., 2016; Ringler et al., 2015). The presence of the species is currently described in the literature as an important indicator of well-preserved forests and landscape conditions because of the habitat requirements to sustain large herds that can be composed by 10s to > 100s of individuals (Beck et al., 2017; Jorge et al., 2013; Keuroghlian and Eaton, 2008a).

In our study systems, we find naturally heterogeneous landscapes that have been affected with different intensity by fragmentation and land cover change, mainly for cattle ranching over the years. Therefore the movement displayed and the area used by WLPs can reveal how modifications in the landscape have impacted habitat quality and availability for the species in those biomes.

More specifically we want to investigate four main questions:

1. *Do WLP herds in the Pantanal and Cerrado display similar patterns of movement and home range?*

   We hypothesize that movement and home range displayed by the herds living in the distinct biomes will be different because the Cerrado areas have been more affected by land cover changes and deforestation in recent years than the Pantanal.

2. *Is there a difference in the movement patterns of male and female WLPs?*

   We hypothesize that movement patterns displayed by males and females will not be divergent and that the main differences will be displayed by the different herds monitored. Although WLPs have a fusion-fission social structure in which males and females of this species could disperse (Biondo et al., 2011), we hypothesize that the movement patterns of herds would be more affected by resource availability than by differences from male and female habitat selection, or for different sex-ratio in the population.

3. *Can we detect different movement modes and average distance traveled per day in the different seasons and regions of study?*

   We hypothesize that movement modes and the average daily distance will be affected by the different seasons due to the differences in resource availability between the wet and dry seasons and that this will reflect in different movement responses for the different herds depending on the landscape context of the different regions of study.

4. *How landscape structure and habitat quality is influencing the herds' space use patterns and can we detect non-optimal movements of WLP in response to landscape modification?*

We hypothesize that herds living in areas more affected by habitat deforestation will face a scenario with a reduced percentage of tree cover availability, with smaller patch sizes and more fragmented; therefore they would have to search for food and other resources in a larger area when the resources in their core areas/main patches are scarce. But WLP will have a limitation of mobility due to avoidance of matrix crossing, which is associated with higher risks of mortality because of human presence and barriers (such as paved roads), so they would only risk leaving their core areas/main patches when the resource is low.

2. MATERIAL AND METHODS

2.1. Study area

Our investigations were developed on two main study regions (Figure 1), in the lowland - Pantanal region (UTM zone 21, 585250 W / 7771000 S) and within the highlands - Cerrado region (UTM zone 21, 677800 W / 7822750 S). The Pantanal is one of the largest wetland in the world (Alho, 2005; Alho et al., 1988; Junk et al., 2006). In Brazil, this biome is located in a central-west portion of the country in the states of Mato Grosso and Mato Grosso do Sul, along the Bolivian border (Alho, 2005; Assine et al., 2015). The Pantanal is a vast expanse of poorly drained lowlands that experiences month-long floods every year during the rainy season from October to April (Junk et al., 2006). Encompassing approximately about 140,000 km^2 in Brazil, the wetland is a mixture of permanent and seasonal swampy areas, but some sand ridges within the wetland are not inundated by floodwaters even during the great floods (Assine et al., 2015). Periods of severe floods are followed by winter and spring drought when only a portion of the Pantanal remains inundated (Hamilton, 2002; Marengo et al., 2016). The vegetation is mainly composed of dry-savanna (which is referred to as Cerrado of Central Brazil), with high densities of natural grass (Pott and Pott, 2004).

The highlands that border the southern Pantanal are comprised largely of sandstone low altitude plateaus (<1000 m) and valleys drained by a dense network of streams. Historically, the Cerrado forest was the predominant type of vegetation cover on the highlands, but currently, the landscape is composed by a mosaic of Cerrado with cash crops and exotic (non-native) pasturelands which currently represent nearly 60% of the land cover (Roque et al., 2016; SOS Pantanal, 2015).

2.2. Capturing procedures

The capture process followed procedures described by Keuroghlian et al. (2004). Box traps (120 L x 90 H x 60 W cm) and wire mesh panel traps were placed in areas frequently used by WLP (indicated by footprints and trails) and baited with salt, corn, ‘‘mandioca’’ (*Manihot* sp.) and local fruits. One camera-trap was set close to the baiting stations to collect data about herd composition and visiting frequencies to the baiting site. VHF trap site trigger alarms from Telonics® were used to monitor capture within a distance for the trapping sites. With this trigger alarms, we could check the status of various traps and reach the triggered trap faster once a WLP was captured.

Once a WLP was caught, the peccary weight was estimated to calculate the amount of anesthesia to be used. Captures and handling of sedated WLP were made following WLP specialist and veterinary instructions, which also checked the heart frequency of the anesthetized individuals and evaluated their health conditions. The individual was sedated in the trap with a TeleDart RD206 injection pistol and a Dart 3 cc syringe with zolazepam–tiletamine (Zoletil, 0,9ml/10kg). Individuals were also marked with a radiofrequency identification microchip (Biomark, Boise, Idaho) to monitor the capture and recapture history. Information of morphometry, sex, weight, and individual age class, defined based on tooth wear (Keuroghlian and Desbiez, 2010; Sowls, 1984), were taken for each individual. Samples of hair and blood for isotopic, genetic and disease analysis were collected for all captured individuals.

After the biometric and collar procedures ended, animals were kept inside the traps for anesthetics’ full recovery, and we released the animals six to twelve hours after sedation. Traps were covered to avoid animals to get stressed while recovering from the anesthetics. Individuals were VHF/GPS tracked after release and we could observe that they re-joined the herds through tracking, observations, and photos from camera-traps; sometimes the herd would stay close to the captured individuals and would only leave after they were released from the traps showing cohesive group behaviour.

2.3. Movement monitoring

WLP herds were monitored between 2013 and 2016 in private properties located in Mato Grosso do Sul state, Brazil (Figure 1). In the plain, southern Pantanal wetlands, the captures and monitoring were made in the municipalities of Miranda and Aquidauana, in four main areas with different landscape compositions at Fazenda 23 de Março, Refúgio Ecológico Caiman (with two main herds monitored in Caiman 1 and 2) and Fazenda Barranco Alto. The economic activities developed in those farms are mainly tourism and cattle ranching. In the plateau, we captured and monitored herds in six different areas in the municipality of Corguinho: one near the Taboco region and the other five at Fazendas Colorado, Jacobina, Santa Tereza, Safira, and Claudia. The main activity in the region is also cattle ranching.

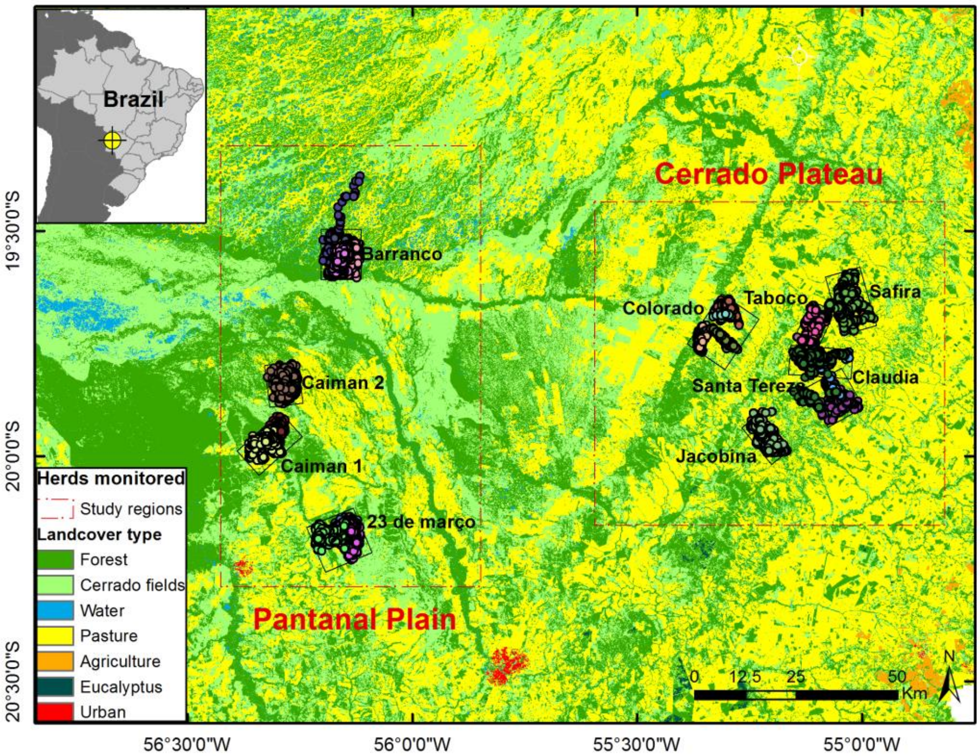

Figure 1. White-lipped peccary herds monitored in the Cerrado plateau (herds: Colorado, Taboco, Jacobina, Safira, Santa Tereza, and Claudia) and in the Pantanal plain (herds: 23 de Março, Caiman 1, Caiman 2 and Barranco Alto) of Mato Grosso do Sul state, Brazil.

Movements of white-lipped peccaries (WLP) were recorded with the GPS/VHF Iridium collars from Followit (Tellus Small total weight of collar ~660 g). We have tried to monitor at least one adult male and one adult female per herd when it was possible, but we had more captures of adult females than males. Collars were programmed to receive from 4 or 8 fixes/individual/day for a maximum of 12 months (~365 days/individual). Satellite data transmission was made every 2 days during the monitoring and information about the WLP positions could be retrieved through the web server from Followit. One individual (Malu) was monitored in two distinct periods because it was recaptured in different seasons, the first period of monitoring was between June and December of 2014, and the second between September of 2015 and March of 2016. Collars had a drop-off system pre-programmed to automatically open the lock after 12 months. We used the Followit battery duration estimate to program the drop off, however not all the collars batteries lasted until the drop off final programming, so once the collars stop communicating via Iridium satellite we did field work campaigns to try to find the individuals with VHF monitoring and recover the GPS-collars with an alternative UHF activated' drop off system.

Individuals were monitored by radio tracking for 7 to 10 days during the field work that was held in dry months. VHF signals were transmitted daily between 9 am to 3 pm to enable herds tracking, checking the collared individuals, resource consumption and herd composition visually during season field work. Areas frequently used were visited to identify foraging and resting sites. Land-use data for ground truth data for mapping was also collected during field work.

2.4. Mapping (GIS) and landscape metrics calculation

Land cover information was based on the 2015 Mapbiomas Collections 1 and 2 datasets (Mapbiomas, 2016) to create simplified land cover map with categories (1- Forest, 2 – Other non-classified cover, 3 – Water, 4 – Natural non-forest vegetation (Cerrado fields), 5 – Pasture, 6 – Agriculture, 7 – Planted Forest, 8 – Coastal Zone vegetation, 24 – Urban). A second raster with only 3 categories was also created based on the Mapbiomas map and tested in the step selection function models (with 3 categories: forest (1), non-forest natural cover (4), matrix (other).

Land cover classification from Mapbiomas was used to select all forest areas (categorie 1) from our study sites and to derive a raster of structural connectivity, considered here as the measurement of the forest patch size structurally connected, and edge distance raster for our study site. Distance from the boundary line between habitat - forest cover - and matrix (hereafter referred to as forest edge) was also calculated based on these patch classifications, using the edges as a zero line as the. Therefore distance had positive values in the matrix and negative values inside the forest patch. The size for the fragment patches and the distances from patch edges were calculated using GRASS GIS extension for connectivity from the Spatial Ecology and Conservation Laboratory (LEEC) - LSMetrics (Niebuhr et al. in prep. https://github.com/LEEClab/LS_METRICS). We have also collected ground truth data during fieldwork to validate and correct the landcover classification.

Percentage of tree canopy cover and forest loss (from 2000 to 2015) was obtained in the Global Forest Change databank - https://earthenginepartners.appspot.com/science-2013-global-forest (Hansen et al., 2013). We have removed all the forest loss area and updated the percent tree canopy cover map for estimates that could reflect better the reality of forest cover for 2015.

The slope data was our topographic variable, we downloaded the raters from TOPODATA website (http://www.webmapit.com.br/inpe/topodata/). This is one of the topographic data derived from Shuttle Radar Topographic Mission (SRTM) which is a radar system based on the interferometry technique that was used to create a Digital elevation model providing topographic information with a 30m resolution for the whole Brazilia territory (Valeriano and Rossetti, 2012).

Two anthropogenic layers were used as proxies for human disturbance and accessibility. One layer was based on the results of human population density information provided by the 2010 census from the Brazilian Institute of Geography and Statistics (IBGE, www.ibge.gov.br). We have downloaded the entire vector data containing the census results that are available in the IBGE ftp server, the data was then rasterized and a mosaic to a single raster (ftp://geoftp.ibge.gov.br/recortes_para_fins_estatisticos/grade_estatistica/censo_2010/). We have also transformed the information of human density in a raster of presence (1) and absence (0) of the human population and calculated the euclidean distance from the human population presence areas. The second layer was the distance from the paved road which was based on the shapefile of existing roads, freely downloaded from the Departamento Nacional de Infra-estrutura de Transportes (DNIT, http://servicos.dnit.gov.br/vgeo/). After classifying the existent paved roads, we calculated the euclidean distance from the roads in all the Brazilian territory in ArcGIS 10.2.

All predictors were rescaled or calculated with cell size set to 900 m^2 resolution and projected to the same projected coordinate system (Universal Transverse Mercator, zone 21S) and datum WGS 84.

2.5. Movement patterns and home range analysis

To prepare data for movement analysis we have excluded the first two days of monitoring because we considered that in this interval WLP movements could be atypical since individuals were still returning from anesthesia procedures, re-joining their herds and getting accustomed with the collars recently deployed. We have also excluded the final days of monitoring when we detected a failure on the collar fix transmission and the intervals of data collection were irregular or inconsistent.

We have first explored descriptive statistical analysis for movement data of all the 30 individuals monitored using the package move v. 3.0.2 (Kranstauber and Smolla, 2018) and UTM zone 21 S projection with datum WGS 84. In a second approach, we have analyzed data only for the individuals that had at least one complete month of monitoring and for which we could regularize fixes for 6 hour intervals (4 fixes per day). As we were dealing with data collected with different schedules, we had to regularize the frequency of fixes to recalculate the month net square displacement and month home range analysis. We have selected only the individuals who had data in a frequency that was possible to be regularized with intervals of 6 hours and after that we interpolated the missing locations if they existed within a burst (sometimes the GPS positions were not sent due to failure when the collar tried to establish contact with the satellite or when the collar was not functioning correctly due to some damage). After that, we recalculated the step sizes, angles (absolute and relative), daily displacement, speed, and net square displacement. Because of this filtering and regularization, we did daily displacement, month net square displacement and month home analysis for 23 individuals.

2.5.1. Daily displacement and Median Speed

Daily displacement and median speed were chosen as response movement variables to compare the patterns of different individuals, different sex (males and females), between the study sites, biomes and seasons, which we defined as dry (which include ebb and dry periods from April to September) and wet (which include flow and wet periods from October to March) (Hamilton, 2002; Junk et al., 2006). Furthermore, we have calculated the net square-displacement using package adehabitatLT (Calenge, 2006) to identify changes residency patterns for white-lipped peccaries during the total period of monitoring and for monthly periods for 24 individuals with regularized data. We have tested for normality ($p > 0.05$) using the Shapiro-Wilk (W) and the Anderson-Darling (A) Normality Tests, and after that, we have applied parametric and non-parametric statistical analysis according to the data distribution identified.

2.5.3. Net squared displacement

The net squared displacement (NSD) is the square value of the distance, measured in a straight-line, from an individual's current location (x0, y0) to its next locations (xt, yt) (Börger and Fryxell, 2013; Turchin, 1998):

$$NSD_{(t)} = (x_t - x_0)^2 + (y_t - y_0)^2$$

The NSD plot over different periods of time can reveal if and when animals display different movement modes. These shifts can indicate periods when an animal is displaying site fidelity within a home range or migrating between seasonal areas of use, or even displaying a nomadic behavior (Börger and Fryxell, 2013). We have evaluated if individuals would present different movement modes using the mean value of the NSD over a month which is defined as the mean net squared displacement (MSD) (Börger and Fryxell, 2013). We have set pre-defined models with different movement behavior modes (nomadic, dispersal, home range, and null) following the expected squared displacement patterns described by Börger and Fryxell (2013). We have tested the model fit to the pre-defined MSD movement models with package nlme (Pinheiro et al., 2019) using goodness-of-fit and the concordance correlation (CC) coefficient for non-linear mixed models, which measures the level of agreement between the observed and predicted values of the model (Börger and Fryxell, 2013; Huang et al., 2009).

2.5.4. Home range analysis

Total home range sizes were measured using three different estimators for GPS data: (1) the minimum convex polygon (MCP) (Powell, 2000), (2) the fixed kernel density estimator with reference bandwidth (HREF) (Börger et al., 2006; Powell, 2000) adjusted for a minimum value to keep only one polygon estimated (for the total area - 95% isopleth and the core area - 50% isopleth), this method will be hereafter referred to as the minimum reference bandwidth kernel density estimator (minHREFK) (Börger et al., 2006; Kie et al., 2010) and we have also estimated home range using the (3) autocorrelated kernel density estimator (AKDE) (Fleming et al., 2015). We have estimated the core areas using the isopleth of 50% of the utility distribution with minHREFK, so that our results could be compared with other study results, and although we know this is an ad hoc definition (Fieberg and Börger, 2012), it is an important measure also to estimate the area where WLPs concentrated their main activities.

The minHREFK was applied to avoid the effects of having a fragmented home range estimate (Börger et al., 2006; Kie et al., 2010), which is usually obtained using a fixed kernel density estimated with the least-square cross-validation to determine the bandwidth (or smoothing parameter) (Fieberg, 2007; Kie et al., 2010; Powell, 2000). As individuals had different periods of monitoring we did also the monthly home range analysis with minHREFK to compare the movement frequencies between individuals, herds, seasons and biomes using regular data (6 hours interval) and the same sample size (30 days) for different individuals.

The AKDE consider the autocorrelation of data collected in a high frequency, it is based on the continuous-time stochastic process (CTSP) models where we separate the movement process from the sampling process (Fleming et al., 2015). To apply the CTPS models we used the ctmm package for R (Calabrese et al., 2016). With this package functions we have done: (i) a variogram plot to evaluate CTSPs, (ii) used maximum likelihood approach to fit CTSP model, (iii) model selection with AIC comparison to choose the best model and estimate the home range with AKDE (Calabrese et al., 2016). The AKDE a semi-variance function to the variogram plot and the three parameters to fit the models (autocorrelation, velocity autocorrelation, and range residency measurements) and estimate the home range size. With those 3 parameters and the AIC based model selection it was possible to classify CTSP models into five different model categories (IID – independent identically distribution, BM – Brownian motion, OU – Ornstein-Uhlenbeck, IOU – Integrated OU, and OUF - Ornstein-Uhlenbeck Foraging) and identify residency or non-resident patterns in the movements observed for WLP (Calabrese et al., 2016; Fleming et al., 2015).

2.5.5. Model Selection

Generalized linear models and non-linear mixed effect models were applied accounting for the biome as random effects for the median speed and daily displacement. We tested different models using landscape measures: percentage of tree cover, patch size, season, distance from fragment edge, and slope. We combined these landscape variables in different models and used the Akaike information criterion corrected values and the model weight to evaluate the proposed models and choose the most plausible model (deltaAIC < 2).

3. RESULTS

3.1. General results

The total number of individuals captured during this study was 105 (67 females and 38 males), from which 45 were captured in the Cerrado region and 60 were captured in Pantanal. Fifty-four individuals were classified as adults by age class and weight, the average biometric measurements for adult individuals in both biomes are shown below in Table 1.

Table 1. Mean biometric measurements for 54 adult white-lipped peccaries captured in Cerrado region and in Pantanal of Mato Grosso do Sul state. Body measures are in centimeters and weight in kilograms.

	Head Body	**Hind Foot**	**Shoulder**	**Neck**	**Ear**	**Tail**	**Gland**	**Age**	**Weight**
Cerrado	110.9	21.0	53.9	55.7	7.3	3.7	20.6	3.2	34.0
Pantanal	113.7	21.4	56.0	55.3	7.1	3.4	21.3	3.3	33.3

Thirty adult white-lipped peccaries received GPS collars, 15 in the Cerrado region and 15 in the Pantanal region, from this total 18 were females and 12 males, and (Table 2). Individuals were GPS/VHF tracked and monitored from 31 to 371 days (Figure 2) although for some individuals due to failures on the equipment we did not have data transmitted for all the period of monitoring. The total number of fixes acquired per individual varied from 40 to 2935 (Table 2). The time of monitoring varied between individuals because collars did not work as expected, we registered three main problems while monitoring WLP with GPS collars: electronic failure (equipment stop sending positions), physical damage on the equipment (mainly in the collar belt) or the battery ending faster than first programmed. We have started this study collecting 4 fixes per day, and we changed the programming schedule for 8 fixes per day but even with reprogramming, collars did not present a regular functioning. Also, two collars were automatically re-programmed to collect 6 fixes per day during the monitoring (individuals Ge and Tainara), what we considered a result of some equipment technical failure.

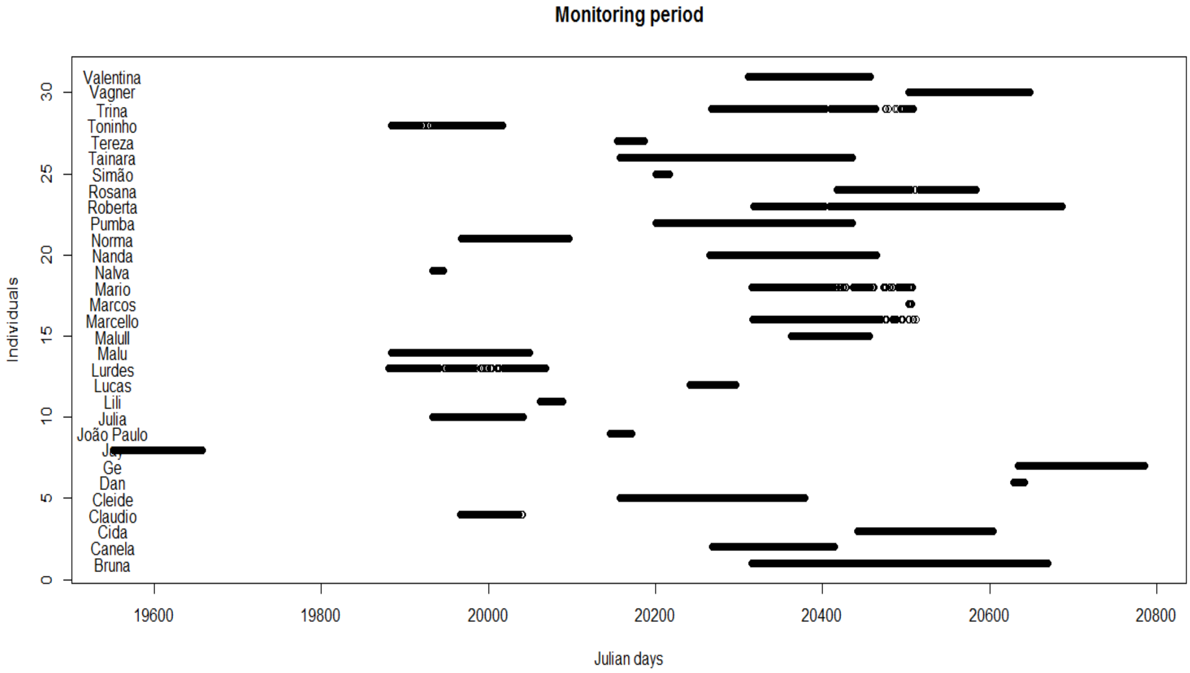

Figure 2. GPS collar monitoring period in Julian days for all white-lipped peccaries that were tracked in Mato Grosso do Sul state, Brazil, between 2013 and 2016.

We also had a different amount of data among the different months the year (Figure 3). Data collected was concentrated in the dry season months because it was when field campaigns were made, therefore most GPS collar deployments started in the dry season due to field work logistic restrictions, and the majority of collars did not last one year as expected, with some exceptions. Therefore we have collected a complete year of monitoring for just a few individuals.

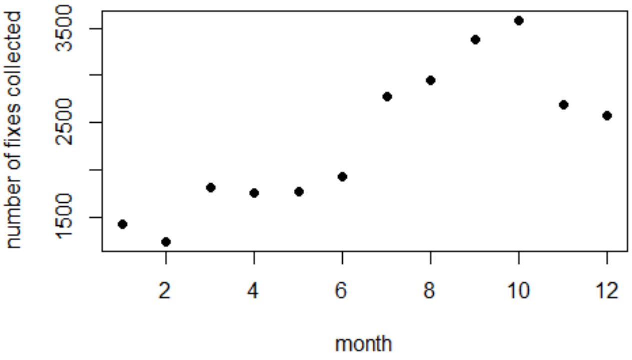

Figure 3. Number of fixes collected by month for all white-lipped peccaries monitored Mato Grosso do Sul state, Brazil, between 2013 and 2016.

3.2. Descriptive movement measures

Movement patterns were analyzed for all white-lipped peccaries' trajectories (Table 4). The mean daily distance moved varied from 1335 to 6013 m (mean = 3501 ± 1801 m) and the median speed varied from 0.012 to 0.049 m/s (mean = 0.03 ± 0.01 m/s). The two metrics are important to quantify movement rates so that we can better describe the movement patterns and habitat requirements for WLP in the two main study regions. In the Cerrado, the mean daily distance registered for WLP was 3098 m while in the Pantanal the mean was 3931 m. The time tracked (in days) was calculated based on the number of fixes successfully transmitted and not on the total number of days that the collar still had battery. Therefore, that time tracked varied among the individuals from 3 to 379 days and the mean time of monitoring per individual was 142 days, the total tracking time was 1842 days in the Cerrado and 2560 days in the Pantanal.

Table 2. Mean daily distance (meters), standard deviation daily distance (meters), median speed (meters/second), time tracked (days) and distance tracked (meters) for adult white-lipped peccaries (Tayassu pecari) monitored in Mato Grosso do Sul state, Brazil, between 2013 and 2016. Here we present non-standardized data because different intervals were used to collect the GPS data for different individuals.

Individual	**Biome**	**Area/Herd**	**Sex**	**Total fixes**	**Fixes/ day**	**Mean dailydist**	**SD dailydist**	**Median speed**	**Time tracked**	**Distance tracked**
Bruna	Pantanal	Caiman 2	F	2797	8	4944	1772	0.04	355	1753825
Canela	Pantanal	Barranco Alto	F	1165	8	4933	1761	0.05	147	723903
Cida	Cerrado	Safira	F	1293	8	2845	1368	0.02	163	462741
Claudio	Pantanal	23 de Março	M	275	4	4149	1432	0.04	74	308072
Cleide	Cerrado	Jacobina	F	1760	8	3682	1386	0.03	222	815546
Dan	Cerrado	Colorado	M	73	8	2608	1355	0.02	14	36518
Ge	Pantanal	Barranco Alto	M	908	8 / 6	4202	1398	0.04	152	640157
Jay	Cerrado	Colorado	M	380	4	2859	1335	0.03	107	304513
Joao Paulo	Cerrado	Colorado	M	310	24 / 12	6013	1771	0.05	27	162609
Julia	Cerrado	Claudia	F	349	4	1703	1376	0.01	109	185211
Lili	Pantanal	Caiman 1	F	113	4	2056	983	0.02	28	56529
Lucas	Pantanal	Barranco Alto	M	457	8	2821	1695	0.02	55	154470
Lurdes	Cerrado	Colorado	F	462	4	1335	1002	0.01	188	251321
Malu	Cerrado	Safira	F	504	4	2312	1143	0.02	167	386086
Malu II	Cerrado	Safira	F	733	8	3763	1796	0.02	93	351396
Marcello	Pantanal	Caiman 1	M	1246	8	3163	1849	0.03	196	619583
Marcos	Cerrado	Taboco	M	40	8	4530	3149	0.04	3	15289
Mario	Pantanal	Caiman 2	M	990	8	3995	2384	0.05	192	768983

Nalva	Cerrado	Claudia	F	60	4	2755	1136	0.02	14	38579
Nanda	Pantanal	Barranco Alto	F	1584	8	4045	1366	0.04	201	811023
Norma	Pantanal	23 de Março	F	507	4	4053	1477	0.04	130	525855
Pumba	Pantanal	23 de Março	F	1800	8	5081	1684	0.05	236	1197814
Roberta	Pantanal	Caiman 1	F	2935	8	4246	1505	0.03	370	1570351
Rosana	Pantanal	23 de Março	F	1240	8	3002	1648	0.03	166	499140
Simao	Pantanal	23 de Março	M	138	8	4540	1265	0.04	17	77748
Tainara	Cerrado	Jacobina	F	1644	8 / 6	3584	1436	0.03	278	997117
Tereza	Cerrado	Santa Tereza	F	110	4	2646	2075	0.03	32	85328
Toninho	Cerrado	Safira	M	397	4	2253	1208	0.02	134	300836
Trina	Pantanal	Barranco Alto	F	1598	8	3739	1483	0.04	242	906347
Vagner	Cerrado	Taboco	M	1151	8	2735	1541	0.02	145	395861
Valentina	Cerrado	Santa Tereza	F	1167	8	3940	1655	0.03	148	581178
Mean						**3501**	**1562**	**0.03**	**142**	**515611**
SD						**1081**	**420**	**0.01**	**96**	**437230**

The mean distance moved per day (daily distance) (W = 0.95693, p-value = 0.3568) and the median speed values (W = 0.95244, p-value = 0.1823) were normally distributed. The log10 cumulative distance moved per day (with 6 hour fix interval) was longer for the individuals monitored in the Pantanal areas (t = -2.1192, df = 22.716, p-value = 0.04522) than in the Cerrado areas (Figure 4 and 5A). Also, the median speed for individuals monitored in the Pantanal was higher than in the Cerrado (t = -3.6177, df = 28.576, p-value = 0.001135) (Figure 6 and 7A). We did not find differences in the mean daily distance moved (t = -0.15061, df = 17.011, p-value = 0.8821) or median speed between males and females (t = -0.72376, df = 23.664, p-value = 0.4763) (Figures 5B and 7B).

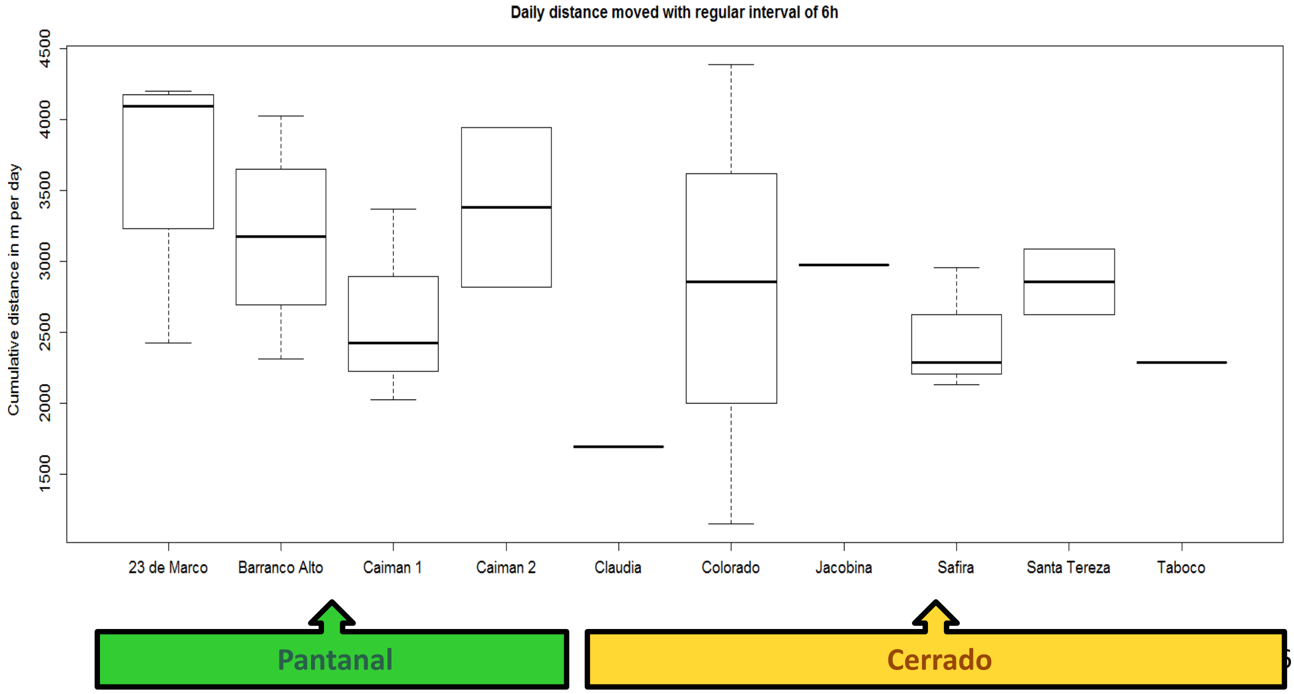

Figure 4. Log10 cumulative distance moved per day for different white-lipped peccary herds monitored in Mato Grosso do Sul state, Brazil, between 2013 and 2016.

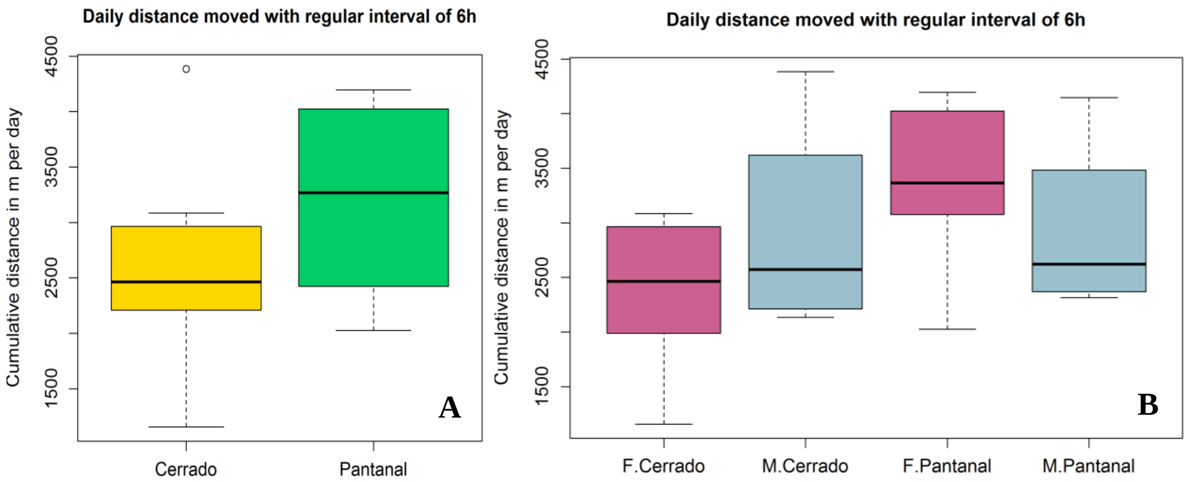

Figure 5. Log10 cumulative distance moved per day for white-lipped peccary herds monitored in Pantanal (green boxplot) was higher than in for the herds monitored in Cerrado (yellow boxplot) of Mato Grosso do Sul state, Brazil, between 2013 and 2016. There is a difference between the daily displacement for individuals living in the different biomes (A) monitored but not between males - M (light blue) and females - F (pink) (B).

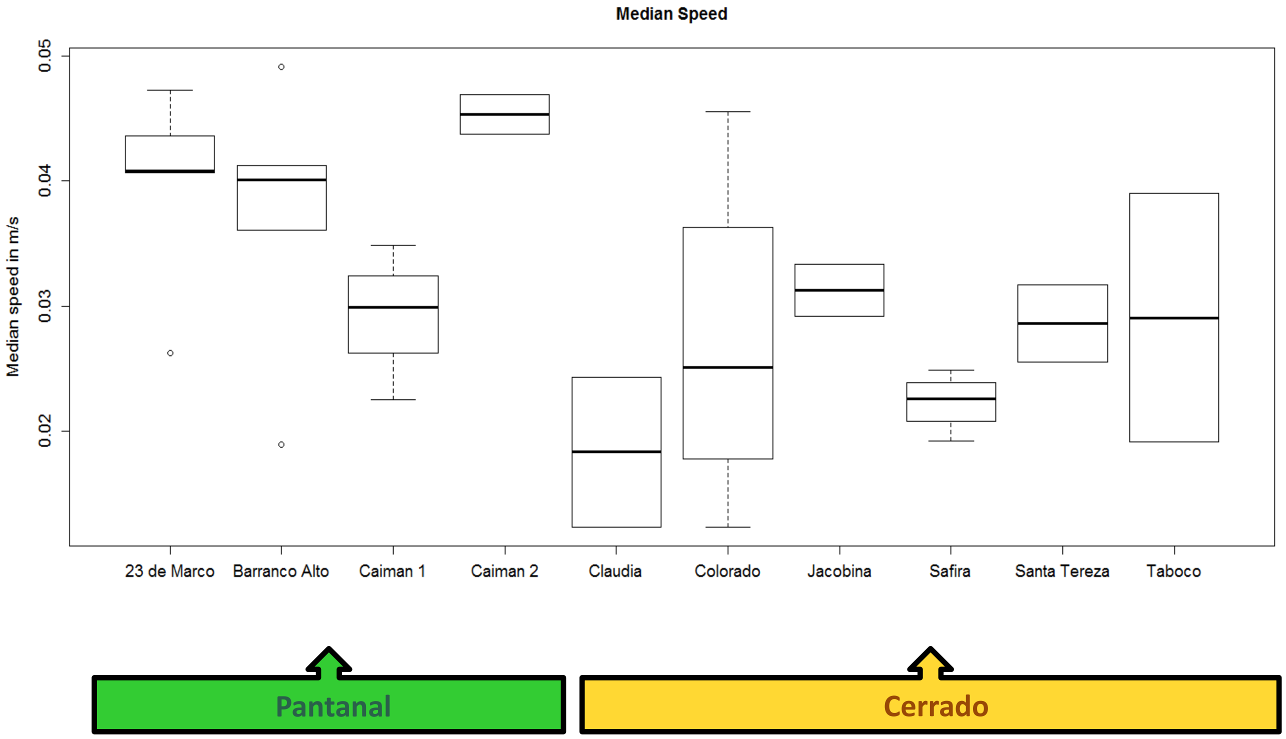

Figure 6. Median speed for white-lipped peccary herds monitored in the Pantanal was higher than in for the herds monitored in Cerrado of Mato Grosso do Sul state, Brazil, between 2013 and 2016.

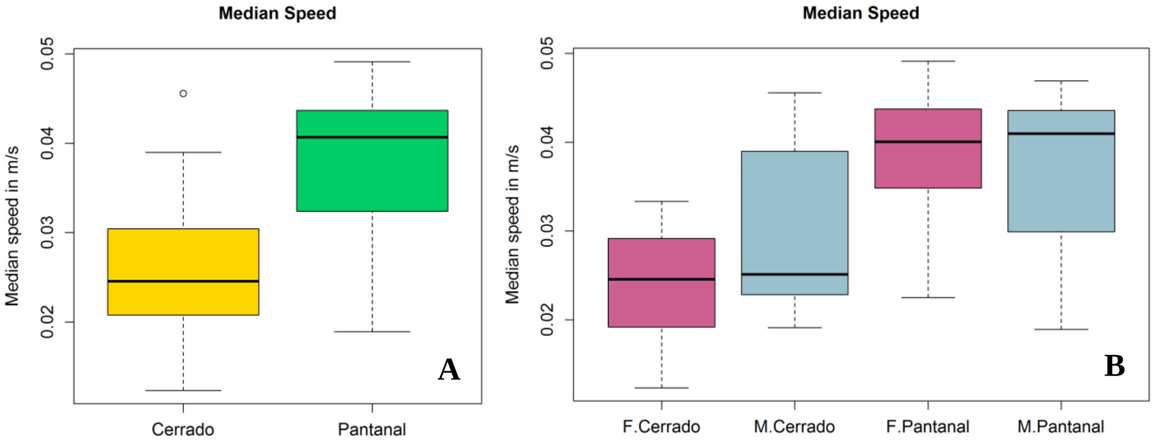

Figure 7. Median speed for white-lipped peccary herds monitored in the Pantanal (green boxplot) was higher than in for the herds monitored in Cerrado (yellow boxplot) - Mato Grosso do Sul state, Brazil, between 2013 and 2016. There is a difference between the median speed for individuals living in the different biomes (A) monitored but not between males (light blue) and females (pink) (B).

We have used AIC multimodel inference, first applying generalized linear models, to evaluate the effect of sex, herd, and biome on daily displacement and median speed for WLP. With this model approach, we could verify that the model composed by Biome and Time tracked was the most plausible to explain both movement metrics. In a second analysis, we have applied generalized mixed effect models with a random effect in the intercept (random intercept) for the Biome variable so that we could test if models with different landscape variables would be more plausible to explain WLP displacement rates. Still, for both metrics, we have verified that the models composed by Biome+Time tracked were the most plausible followed by the model with Biome + Time tracked + Slope effects (Supplementary material).

3.3. Home range analysis

We estimated the total home range size for each individual using the MCP (mean = 28.16 ± 18.72 km^2), the minHREFK (mean = 32.98 ± 21.75 km^2) and the AKDE (mean = 52.59 ± 41.40 km^2) (Table 3). In the Cerrado, the total home range size estimated for each WLP with the MCP had mean of 33.31 ± 23.49 km^2, with the minHREFK mean of 40.47 ±

26.36 km^2 and with the AKDE mean of 71.42 ± 48.64 km^2 (Table 3). In the Pantanal, the total home range size estimated for each WLP the MCP had mean of 23.01 ± 10.48 km^2, with the minHREFK mean of 25.49 ± 12.86 km^2 and with the AKDE mean of 33.76 ± 20.61 km^2 (Table 3). The core areas were estimated with the minHREFK and had an average size of 7 km^2 (± 5 km^2).

For the three different estimators, the average home range size for WLP was larger in the Cerrado than in the Pantanal (Supplementary material) but only with the AKDE, we have found significative differences between the mean values for the 2 biomes (W = 168, p-value = 0.0209). We have also verified differences on the total home range size between males and females using the three different methods tested, which is more evident between the home range size of the Cerrado males and females (**minHREFK** - W = 168, p-value = 0.01015, **MCP** - W = 174, p-value = 0.004291, **AKDE** - W = 171, p-value = 0.006682).

The AKDE presented the highest values of home range size, as already expected since this method accounts for autocorrelation, and larger areas were estimated with this model because it is set based on the variogram parameters, adjusting the best movement model to estimate a home range area. Also, the parameters of the AKDE are informative (Table 3), tau.position represents the **home range crossing time**, therefore WLP crosses their entire home range area within one week on average (mean = 7.05 ± 6.28 days). The tau.velocity indicates the **velocity autocorrelation timescale**, which can be interpreted as the time period in which WLPs were keeping the movement in the same direction with autocorrelated velocities (mean = 29.09 ± 21.57 minutes). The speed indicates the **average distance traveled** in a day (mean = 9.24 ± 2.77 km /day), which is longer than the values calculated with the WLP trajectories and not accounting for autocorrelation.

We used AIC model selection to define the best model fit and for the majority of the WLPs monitored, we could estimate the AKDE with an OUF model (Ornstein-Uhlenbeck Foraging process model). OUF model indicates a restricted space of use (home range behavior) and data for which it was possible to estimate the directional persistence through the velocity correlation. For five individuals the best-fitted model was the OU (Ornstein-Uhlenbeck process model) which indicates a Brownian motion model with some evidence of restricted use of space. Therefore, for those five datasets, the movement was composed by diffuse trajectories without evidence of directional persistence, which cannot be estimated in those cases (Calabrese et al., 2016).

We have also evaluated the monthly home range using the minHREFK. The average monthly home range for WLP, estimated with regularized data in a 6h interval, was 26.63 ± 21.95 km^2 (Supplementary material). Monthly home range varied from 3.95 km^2 (Lurdes_2) to 143.60 km^2 (Valentina_3). The average monthly home range was also larger for the WLP living in the Cerrado (mean = 34.02 ± 31.08 km^2) than for the WLP living in the Pantanal (mean = 21.89 ± 11.09 km^2) but with no significative differences (W = 1702.5, p-value = 0.1092) (Figure 8). Therefore, for average monthly home range with regular sampling data, we also found that individuals presented larger areas of use in the Cerrado than in Pantanal.

Table 3. Home ranges for WLP herds monitored between 2013 and 2016 in the Cerrado and Pantanal of Mato Grosso do Sul, Brazil.

Individual	**Biome**	**Area/Herd**	**Sex**	**MinHREFK 50%**	**MinHREFK 95%**	**MCP**	**AKDE results**					
							AKDE	**best.model**	**dAICc**	**tau.position**	**tau.velocity**	**speed**
Bruna	Pantanal	Caiman 2	F	4.63	28.19	28.22	26.12	OUF anisotropic	114.90	16.86	45.88	11.38
Canela	Pantanal	Barranco Alto	F	6.97	46.53	44.32	83.34	OUF anisotropic	66.79	2.46	48.99	10.48
Cida	Cerrado	Safira	F	18.89	78.29	60.88	103.13	OUF anisotropic	2.25	7.03	49.71	6.73
Claudio	Pantanal	23 de Marco	M	8.28	30.96	22.66	32.97	OUF anisotropic	19.31	14.79	2.32	8.17
Cleide	Cerrado	Jacobina	F	7.78	35.42	36.02	90.67	OUF anisotropic	45.34	4.24	44.81	8.60
Dan	Cerrado	Colorado	M	1.36	6.26	2.83	5.90	OU anisotropic	2.23	7.69	NA	NA
Ge	Pantanal	Barranco Alto	M	3.70	17.18	19.02	22.50	OUF anisotropic	3.30	20.30	28.55	12.59
Jay	Cerrado	Colorado	M	7.06	25.94	18.50	38.05	OUF anisotropic	16.44	1.47	1.67	6.48
Joao Paulo	Cerrado	Colorado	M	2.12	9.04	7.42	16.66	OUF anisotropic	24.07	15.33	33.99	13.71
Julia	Cerrado	Claudia	F	14.87	65.62	43.30	78.57	OUF anisotropic	3.24	6.75	51.83	5.98
Lili	Pantanal	Caiman 1	F	0.65	4.01	1.76	3.43	OUF anisotropic	0.23	3.12	3.12	4.84
Lucas	Pantanal	Barranco Alto	M	2.26	16.27	11.17	19.48	OUF anisotropic	4.50	1.36	44.81	7.03
Lurdes	Cerrado	Colorado	F	5.44	24.19	15.08	44.51	OU isotropic	0.48	6.66	NA	NA
Malu	Cerrado	Safira	F	11.01	57.30	48.20	65.46	OU anisotropic	1.01	3.57	NA	NA
Marcello	Pantanal	Caiman 1	M	2.99	17.74	17.37	21.18	OUF anisotropic	1.38	1.05	14.40	14.86
Marcos	Cerrado	Taboco	M	2.26	12.90	4.30	13.68	OUF anisotropic	2.07	8.88	1.75	7.95
Mario	Pantanal	Caiman 2	M	4.26	24.32	22.55	23.60	OUF anisotropic	17.02	12.27	36.21	14.39
Nalva	Cerrado	Claudia	F	6.28	22.16	15.96	56.33	OU anisotropic	1.55	3.79	NA	NA
Nanda	Pantanal	Barranco Alto	F	4.07	16.48	19.59	30.44	OUF anisotropic	24.97	1.37	29.93	10.90
Norma	Pantanal	23 de Marco	F	13.70	50.12	35.02	66.25	OUF isotropic	4.03	1.68	1.30	8.79
Pumba	Pantanal	23 de Marco	F	11.77	44.19	37.96	60.45	OUF anisotropic	7.19	1.43	58.88	10.49
Roberta	Pantanal	Caiman 1	F	4.36	27.78	29.75	35.15	OUF anisotropic	11.82	1.27	37.44	10.64
Rosana	Pantanal	23 de Marco	F	4.52	22.24	21.30	26.01	OUF anisotropic	1.81	1.48	59.36	6.73
Simao	Pantanal	23 de Marco	M	3.61	18.15	13.63	29.05	OUF anisotropic	1.96	20.92	1.12	8.80
Tainara	Cerrado	Jacobina	F	7.27	31.99	35.07	83.44	OUF anisotropic	20.44	3.81	35.33	9.78
Tereza	Cerrado	Santa Tereza	F	20.57	86.97	71.42	192.45	OUF anisotropic	9.07	6.33	2.44	5.91
Toninho	Cerrado	Safira	M	6.66	43.19	33.62	52.51	OU anisotropic	2.06	3.52	NA	NA
Trina	Pantanal	Barranco Alto	F	4.86	18.23	20.81	26.50	OUF anisotropic	115.95	20.05	59.06	9.24
Vagner	Cerrado	Taboco	M	5.95	31.25	30.41	111.56	OUF anisotropic	44.78	6.88	1.21	5.92
Valentina	Cerrado	Santa Tereza	F	13.79	76.47	76.65	118.43	OUF anisotropic	25.89	5.07	33.05	10.51
Mean				**7.06**	**32.98**	**28.16**	**52.59**		**19.87**	**7.05**	**29.09**	**9.24**
SD				**5.06**	**21.75**	**18.72**	**41.40**		**30.46**	**6.28**	**21.57**	**2.77**

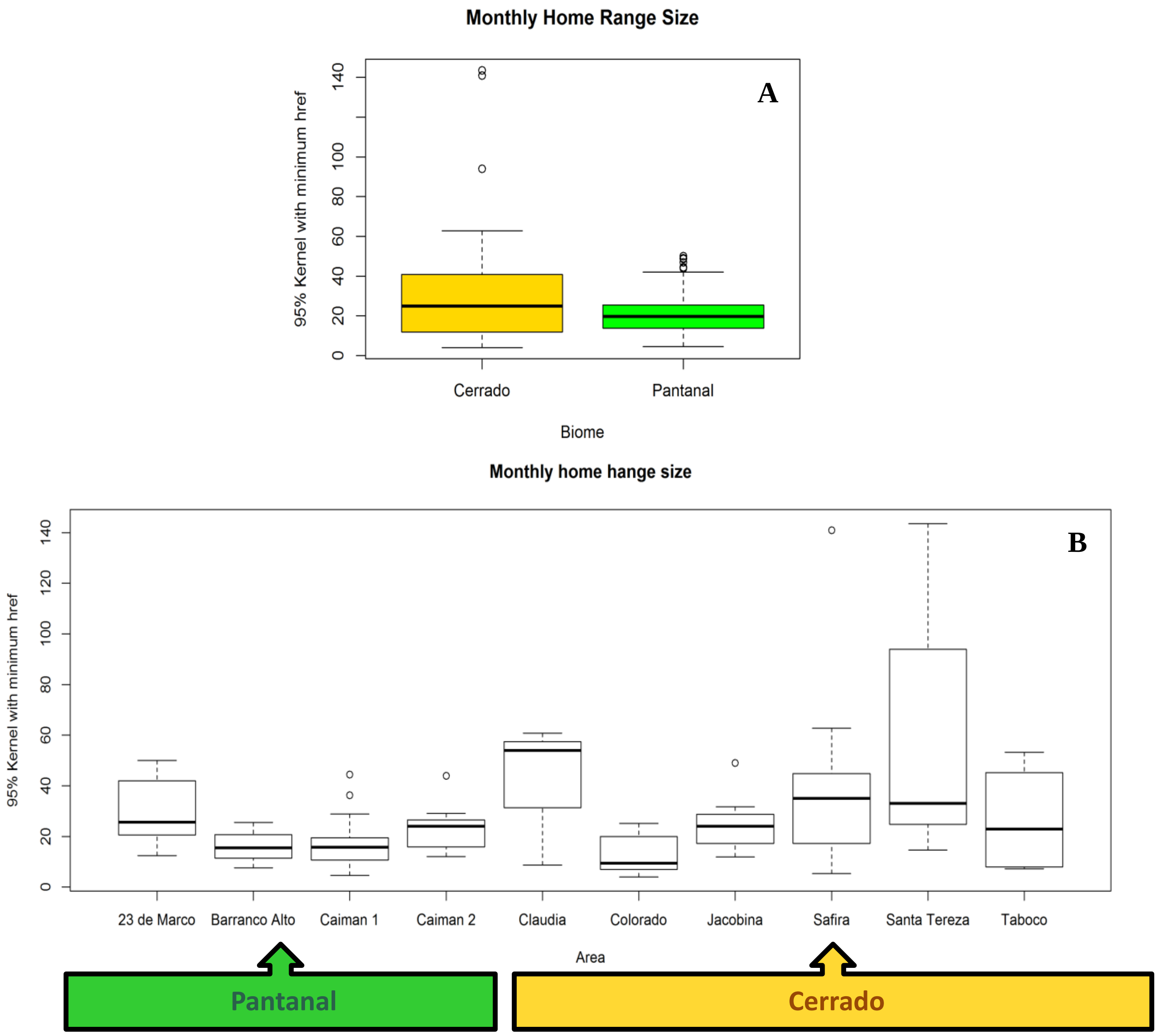

Figure 8. Monthly home ranges (A) for WLP herds (B) monitored in the Cerrado were larger than the monthly home ranges for WLP herds monitored in Pantanal during our study in Mato Grosso do Sul state, Brazil, between 2013 and 2016.

3.3. Net Square displacement analysis

We have also analyzed the net square displacement variation among individuals using regularized data for an interval of 6h between fixes, and it was possible to verify that most individuals showed a resident pattern with some expansion of the home range seasonally. Only two individuals did long-distance movements with returning to the original home range site (Valentina and Tereza), therefore showing some occasional explorative movements and resulting in seasonal expansion of the areas used.

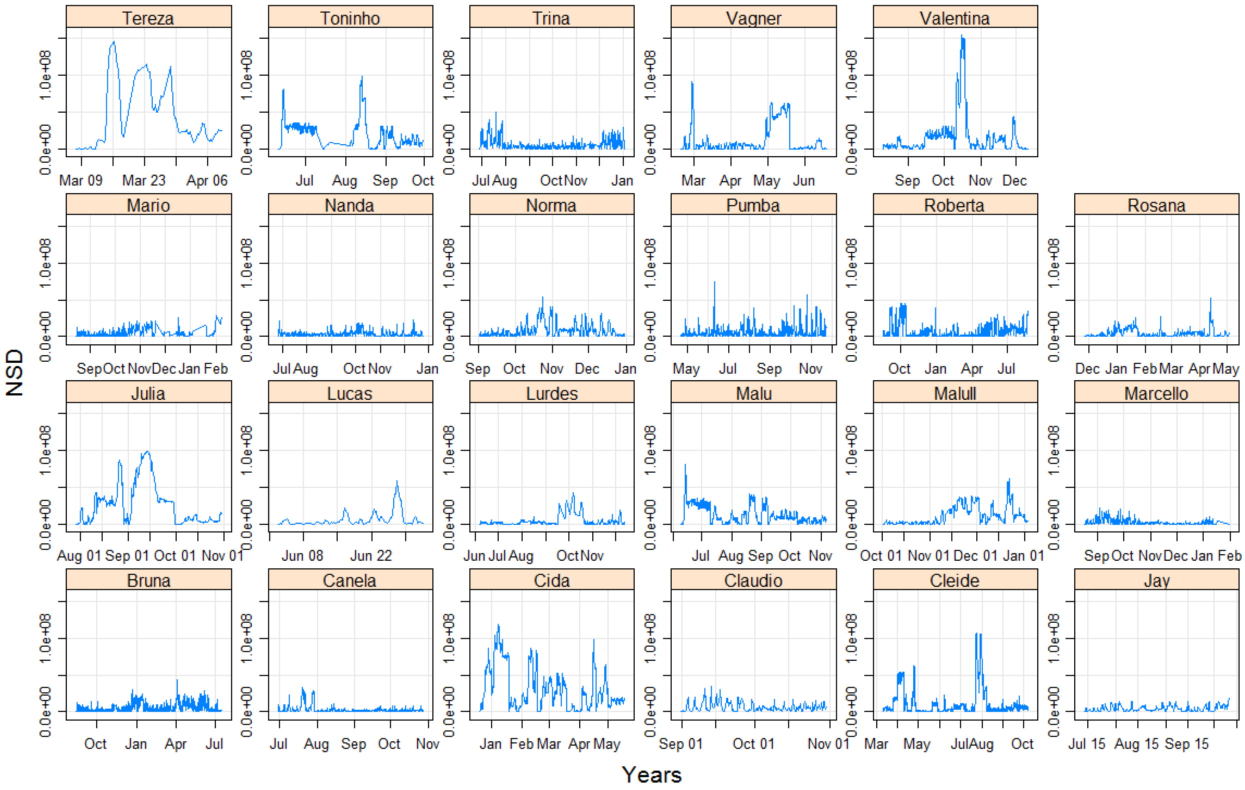

Figure 9. Net square displacement with regularized data (6h interval between fixes) for 23 white-lipped peccary individuals monitored in Mato Grosso do Sul state, Brazil, between 2013 and 2016.

The NSD values (with 6 hour fix interval) were not normally distributed (A = 1550.7, p-value < 2.2e-16). We have detected differences in the NSD values between the dry and wet seasons (W = 20148000, p-value = 0.01193) (Figure 10A and Supplementary material). NSD values were higher for individuals monitored in the Cerrado areas (W = 23731000, p-value < 2.2e-16) than in the Pantanal areas (Figure 10B and Supplementary material). Although, the Colorado herd in the Cerrado presented NSD values similar to the Pantanal herds.

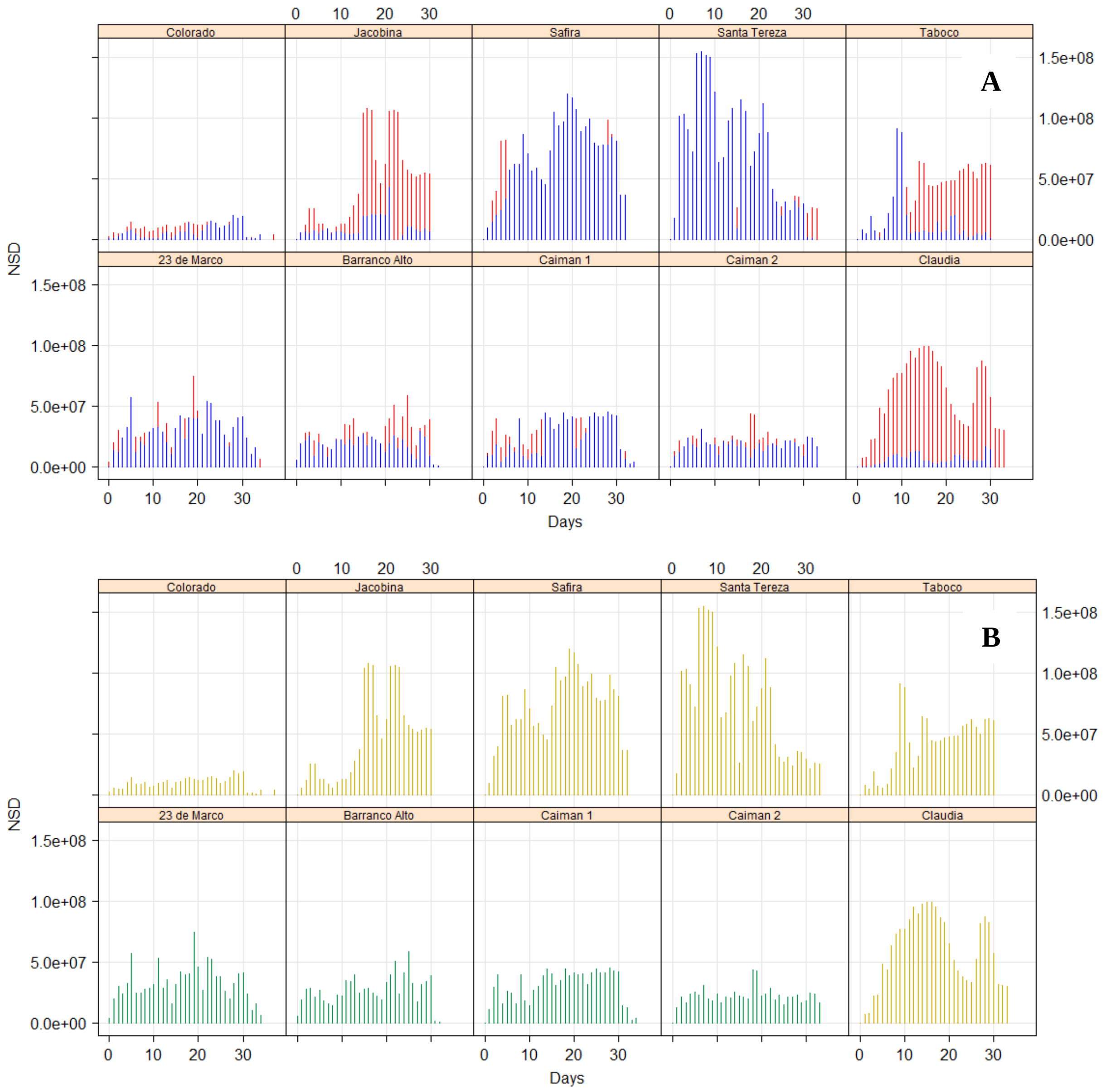

Figure 10. Monthly net square displacement analysis for white-lipped peccary herds monitored in the (A): dry (red) and wet season (blue) and in the (B): Cerrado (yellow) and Pantanal (green) of Mato Grosso do Sul state, Brazil, between 2013 and 2016.

We have used the MSD model selection analysis to verify changes in the movement modes for the monthly NSD values with linear mixed effect models. Monthly MSD analysis revealed that WLP can present nomadic and dispersal behavior in this specific scale of time (30 days with 4 fixes per day). Dispersal monthly behavior was more commonly observed for individuals in the Cerrado and Nomadic monthly behavior was more common for individuals living in the Pantanal region (Figure 11).

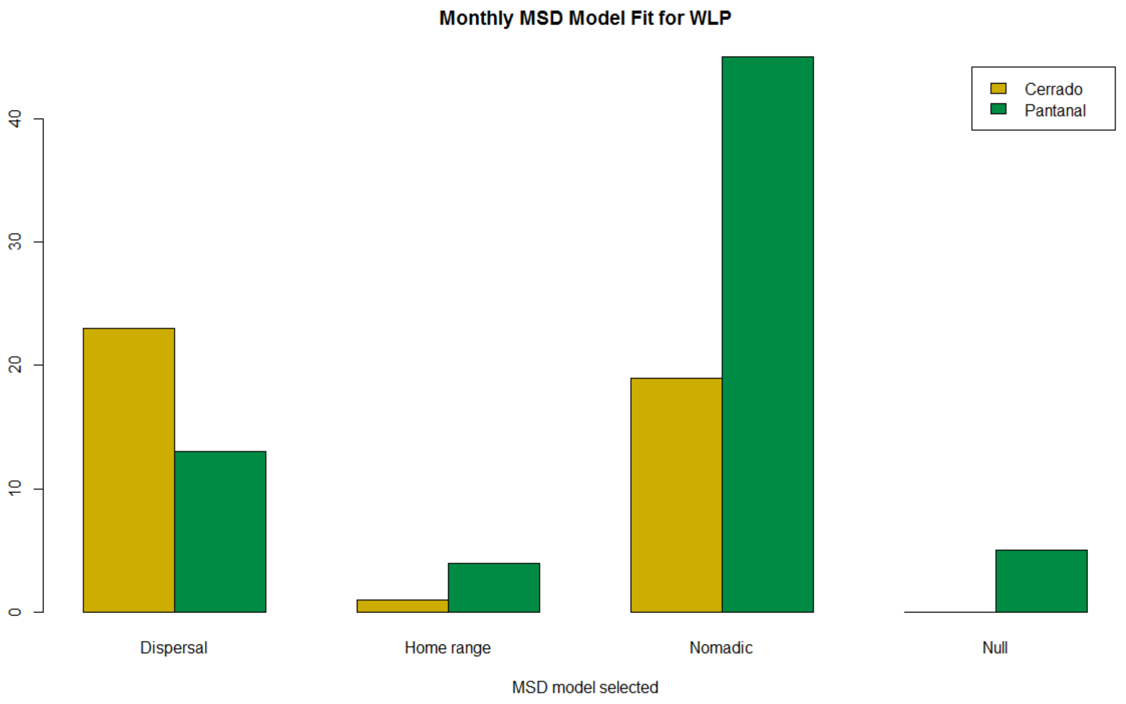

Figure 11. Monthly mean net square displacement results showing the number of the white-lipped peccary monthly data classified in each movement behaviour category. Herds were monitored in the: Cerrado (yellow) and Pantanal (green) of Mato Grosso do Sul state, Brazil, between 2013 and 2016.

4. DISCUSSION

The WLP is a keystone ungulate species that has been rapidly extirpated from Neotropical forests (Altrichter et al., 2012) and information about its space use from fine-scale GPS data is still scarce but crucial to evaluate if changes in the landscape structure and habitat quality are currently influencing the species movements and home range in the areas where it still exists. We have explored movement patterns and home range for WLP in two important biomes of Brazil and we have found that the mean daily distance for 30 tracked individuals was 3501m, with the median speed of 0.031m/s (or 111.6 m/h). We have also found that the home range size had mean values varying depending on the estimator used: 28 km^2 (MCP), 33 km^2 (minHREFK) and 52 km^2 (AKDE). Accounting for autocorrelation using CTPS models (AKDE) for home range estimation showed that the majority of individuals have established a restrict space use (OUF model), during the time that we have monitored them (1 -12 months), which characterized home range behavior. But it also showed that the areas required for WLP to live can be even larger than it is usually estimated with the traditional methods used (e.g. MCP and Kernel density estimator).

The home range estimation have the intent to give researchers a hint about the individuals cognitive map (Powell and Mitchell, 2012), and the WLP has shown to require large areas with high amount forest cover to survive, what have been also shown by previous studies (Fragoso, 1998, 2004; Hofman et al., 2016; Jácomo et al., 2013; Jorge et al., 2019; Keuroghlian et al., 2004; Reyna-Hurtado et al., 2009). Our results corroborate these previous studies results as we have shown that the WLPs were using areas with the average size of 50 km^2 (AKDE), and that varied from 3.5 to 192 km^2, in different landscapes of our study regions. WLP is known to be the tropical forest ungulates with the largest home ranges (Fragoso, 2004; Reyna-Hurtado et al., 2012), so they are highly–mobile and explore large areas to reach all the resources that they need, and even the average core area size, which we have estimated in 7 km^2 (50% minHREFK), can be considered large when compared with other neotropical mammals' home ranges.

4.1. Seasonal changes in resource availability impact on WLP movement

As frugivorous-omnivorous ungulates, WLPs have to search for resources with a patchy distribution (Reyna-Hurtado et al., 2012) to fulfill large herds. When the availability of fruits, water, and air temperature change seasonally, these resource fluctuations affect WLP feeding habits, foraging strategies, activity patterns and movement (Hofmann et al., 2016; Keuroghlian et al., 2009; Reyna-Hurtado et al., 2012). In the dry season, WLP living in the northern Pantanal change their activity patterns by increasing the activity during the night, and reducing it between 10 am to 3 pm to avoid higher air temperatures during the day (Hofmann et al., 2016). In our study region, fruit diversity and quantity decreases in the dry season (Keuroghlian et al., 2009), this change in resource availability affects the intra-patch habitat quality and could obligate individuals to expand their foraging search area in periods of resource scarcity. That could have three distinct effects: (1) WLPs would have to cross matrix areas to search for resources in new patches or (2) WLPs would stay in a unique large patch but would change their foraging search strategy, they could change their core areas inside the patch seasonally. Resources would be more sparsely distributed but would still be enough for WLPs to stay in the same patch avoiding to cross matrix areas to search for new patches or (3) WLPs would be trapped in a forest fragment because there are no other patches in a functional distance that would allow them to cross the matrix surrounding the patch, therefore the population would be isolated in a forest patch. In the first scenario, WLP would have expanded their home ranges (if they could cross the matrix), in the second scenario WLP could change their movement rates (increase searching) and range size (change in core areas) within a single patch, and in the third scenario, they would explore the whole patch. The decision to move or to stay in a patch is a trade-off decision depending on the habitat quality within the occupied patch and the difficulties or risks imposed by the matrix, given by the landscape structure in which the herds are living, as discussed in Doherty and Driscoll (2018).

In a recent study, Jorge et al. (2019) have shown a positive effect of the number of fruiting tree species on WLP range sizes from the Cerrado areas, but differences between range size, estimated with MCP, in the different seasons was not detected. In our study, differences among average WLPs home range sizes estimated with AKDE were detected when comparing the two biomes and differences between seasonal use were verified for the NSD values. Which means that differences of seasonal resource availability (food, water and/or other resources) can motivate WLPs to explore different regions, closer or further away from their home range centroid.

4.2. WLP space use in different biomes

We have shown that WLPs in the Cerrado are displaying different movement patterns and home range from WLPs from the Pantanal areas. While the average distance moved per day and the average median speeds were higher for the individuals monitored in the Pantanal than for the individuals monitored in the Cerrado, the average home range size and the average NSD were higher for the individuals in the Cerrado than for the individuals in the Pantanal. WLPs from the Pantanal are displaying higher mobility rates without having to expand their home ranges, while in the Cerrado WLPs are using larger areas and they are moving less per day. When we tested the effect of landscape variables in the daily distance and for median speed of WLPs, we have seen that slope and percent of tree cover are playing important roles in the mobility rates.

Our results indicate that differences in the mobility of WLPs in the Cerrado and Pantanal of the Upper Paraguay River Basin (UPRB) were affected by the geomorphological characteristics of their habitats. The Pantanal wetlands are naturally formed in the plain' flat terrains, which facilitate WLPs (and other mammals) displacement. While in the Cerrado, the topography is composed by steeper slope terrains of the plateau, which naturally increase the difficulty for displacement (Supplementary material). Moreover, the deforestation in the two regions has been historically different, with land conversion acting faster in the Cerrado than in Pantanal, due to the difficulties to develop economic activities in areas that are affected by seasonal inundations in the past, but currently 80% of the Pantanal lands are used for cattle ranching which is raised mostly extensively (Silva et al., 2011). We could observe that in the Pantanal WLPs explored more areas outside the fragments boundaries, especially the Caiman herds, which also used the regions with a smaller percentage of tree cover (Supplementary material). We have observed that this was a direct effect of the main activity developed in the farm, which is focused on the wildlife observation tourism and WLPs present a more bold behavior to the presence of humans, which also influenced their movement towards human-modified landscapes. The absence of dogs in Caiman and Barranco Alto farms, as well as the environmental education for tourists in Pantanal, were important tools to reduce the conflicts between human and wildlife in a local context and also showed an impact on the space use of WLPs.

In the UPRB, the land has been mostly converted for cattle ranching and through the use of fire to clean natural grassland in the Pantanal areas in the last 300 years (Hamilton, 2002; Prance and Schaller, 1982), what have affected vegetation composition and distribution. In recent years, deforestation has increased considerably in the UPRB, where 60% of the planning units have currently less than 40% of native vegetation cover (Roque et al., 2016), and if the speed in which land conversion continues with the historical patterns of deforestation observed in the last decades, it is estimated that all the native vegetation will be lost by 2029 in the plateau and by 2045 in the floodplain (Silva et al., 2011). Besides, more than 95% of the Pantanal is composed private properties (Silva et al., 2011), and only 2,5% of the UPRB have protected areas (Harris et al., 2005).

In the Cerrado, most of the forest fragments are located in areas of legal reserve or in regions that are protected by the forest code (Soares-Filho et al., 2014), which prioritize areas for protection against deforestation, mainly riparian vegetation and forest fragments within steep slope terrains. Consequently, in the Cerrado, the areas where we find the largest and more connected fragments are located into the valleys near the Serra do Maracaju scarps, the region that is mostly used by the Colorado herd. For the other herds in the Cerrado, the riparian vegetation was essential to keep the connection between distinct fragments and WLPs have used these regions for displacement among forest patches.

4.3. Male and females WLP can have different movement patterns?

It has been suggested that dispersal for male and female WLPs is possible and that the dispersal rates could be affected by the sex-ratio in the population, and the consequent increase in the intra-herd resource competition among individuals from the same sex and male competition over females (Biondo et al., 2011). As different studies have shown female biased sex-ratio for WLP populations (e.g. Altrichter et al., 2001; Biondo et al., 2011; Jácomo, 2004), and we have also verified higher capture rates for females than males in our study, it could be expected to observe higher competition among females with a higher rate of females dispersal than males dispersal (Biondo et al., 2011). We have tested for differences in movement patterns and home range of males and females, searching for these hypothetical differences that could happen due to differences in dispersal rates. Different from what we hypothesize, we did not find differences in the movement patterns, but we did find differences in the total home range size and in the NSD results between of males and females. Although results could be affected by the fact that we only monitored males from the Taboco herd and only females from the Santa Tereza, Jacobina and in Claudia herds. Besides, the WLPs from Santa Tereza herd were the individuals with the largest home ranges. We would need more data from males and females monitored in the same period to really claim that those differences are detected within the same herds.

4.4. Movement behavior can change in different temporal scales?

Monthly home range size had an average of 26 km^2 (minHREFK) and the mean NSD analysis applied for monthly data showed that, although WLP usually display a home range behavior when we look for the entire trajectory of each individual, the movement mode can change among different months and in this scale of time (30 days) we can identify mostly nomadic and dispersal behaviors. Monthly changes on the movement behavior can be associated also with changes in the resource availability within the patches or seasonal resource availability which would individuals to explore more patches. The AKDE showed that most WLPs can cross their entire home range area within one week on average, therefore they could explore different regions within the home range in 30 days.

Analyzing movement and home range behavior of individuals in different biomes and scales of time and space can drive different conclusion about the habitat requirements for the species persistence and that information is essential for the species conservation in heterogeneous productive landscapes. Finally, despite the progress on the habitat selection and movement ecology research that have been developed for WLP, much work is still needed to account for the types of movement behavior often observed in this and other long-lived species with spatial memory, learned behavior and complex social structure (Fryxell et al., 2008; Morales et al., 2004; Mueller and Fagan, 2008). Therefore the study of the WLP habitat selection and movement addresses new information for movement ecology itself and may provide answers about what are the habitat-specific parameters and the traits of large social mammals that influence their population persistence in altered landscapes.

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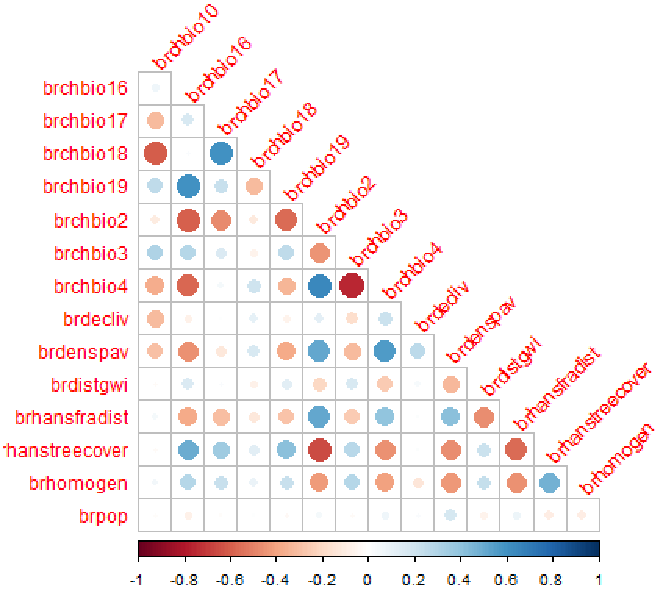
CONCLUSION

In this study, we brought new information about white-lipped peccary (*Tayassu pecari*) distribution and movements explored in different scales and biomes of Brazil. We investigated which landscape variables would influence the species space use in different scales and orders of selection. Our results represent an important step to evaluate where are the remaining suitable areas for WLPs in Brazil, providing spatial information about how landscape modifications and anthropogenic pressure is affecting the species persistence. This is essential to determine the species current conservation status and to define more efficient conservation actions, such as defining new areas for population surveys and monitoring, placement of ecological corridors and target regions for educational programs that seek to reduce habitat loss and illegal hunting. Finally, our models showed that *T. pecari* responds to landscape changes and have been losing habitat in recent years with only 47% of Brazil remaining with suitable areas for the species. Forest loss in Brazil impacted 337,318 km^2 that were suitable for the species in the last decade and only half of all protected areas in the Cerrado and the Atlantic Forest biomes have suitable habitat for the species. With the movement analysis, we showed that higher percent of tree cover, larger forest patches, proximity to water sources and proximity with fragment center had a positive effect on habitat selection by white-lipped peccaries. But the species avoided steep slope areas, paved roads, and areas of higher population density. We showed that riparian areas are essential to improve functional connectivity for the species and that the matrix crossing distance for pasture cover did not exceed 700m, which means that connectivity for *T. pecari* can be limited by land cover, paved roads, and highly populated regions. This information can be applied to determine new conservation management actions in our study region. As previous studies have also shown, white-lipped peccaries are highly mobile moving on average 3501m per day in our study region. The total home range size can be affected by the estimator used and in our study, it was 52 km^2 (AKDE) on average. Considering autocorrelation in the home range estimates was important to verify that the species can require even larger areas than previously expected. With this study, we could identify that seasonal changes in resources and in the landscape structure can trigger changes in the movement patterns and in the home range during the animals' lifetime. Analyzing movement and home range behavior of individuals in different biomes and scales of time and space can drive different conclusions about the habitat requirements for the species persistence, and that information is essential for its conservation in heterogeneous productive landscapes. Monitoring movements of *T. pecari* can be challenging and safety procedures aiming animal welfare during capture and tracking of white-lipped peccaries should be considered for future studies. Our research also provided data to fill in some gaps about wildlife GPS tracking information that was incorporated in a collaborative manuscript recently published about the performance of satellite telemetry in terrestrial wildlife research by Hofman et al. 2019 in Plos One. In that document there are recommendations for both researchears and manufactures working with wildlife telemetry. Finally, despite the progress on the habitat selection and movement ecology research that have been developed for WLP, much work is still needed so we can better understand how spatial memory, learned behavior and social organization is influencing the species spatial use. Therefore the study of the WLP habitat selection and movement addresses new information for movement ecology itself and may provide answers about what are the habitat-specific parameters and the traits of large social mammals that influence their population persistence in altered landscapes.

SMC1. SUPPLEMENTARY MATERIAL OF CHAPTER 1

SM1 Results from the Pearson correlation analysis.

Correlation between tested variables



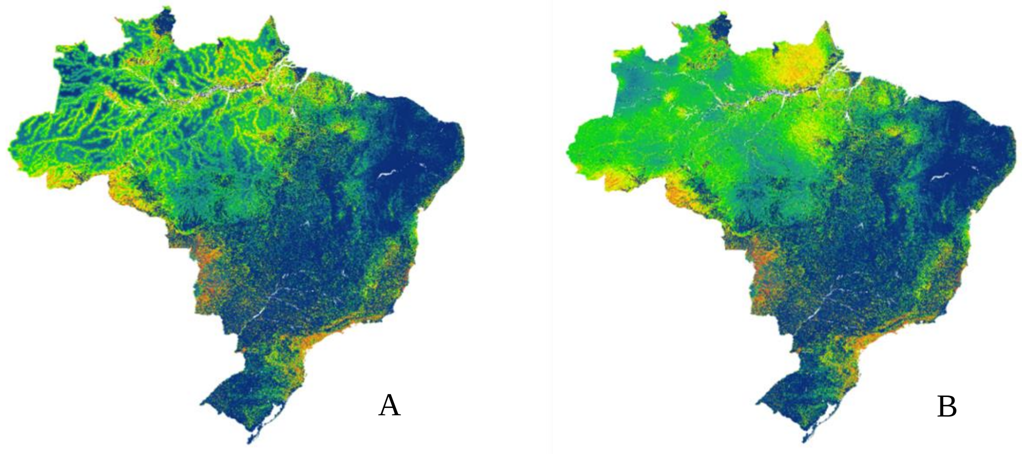
SM2 Bias correction test

Our tests for bias correction showed that none of the layers used for bias correction provided better Maxent model estimates. Therefore, we used just spatial and environmental rarefaction for excluding clumped and duplicated points, with proximity and sharing of the same heterogeneity class layer as rules for excluding similar information for spatially close presence records (see Spatial and environmental rarefaction of occurrence data section in Methods). We did not use any biased prior for correction by access routes (density of rivers in Amazon and paved roads in the other regions), or kernel density for the presence data in the final models. And although edge distance variable improved models AUC and AICc (Table SM1), after visually analyzing the final map outputs (Supplementary material), we concluded that the variable was generating an overfitting of the model because of sampling bias near Amazon rivers, and that the models without distance variables were providing more biologically meaningful predictions, therefore, we decided to keep the final estimations without this predictor.

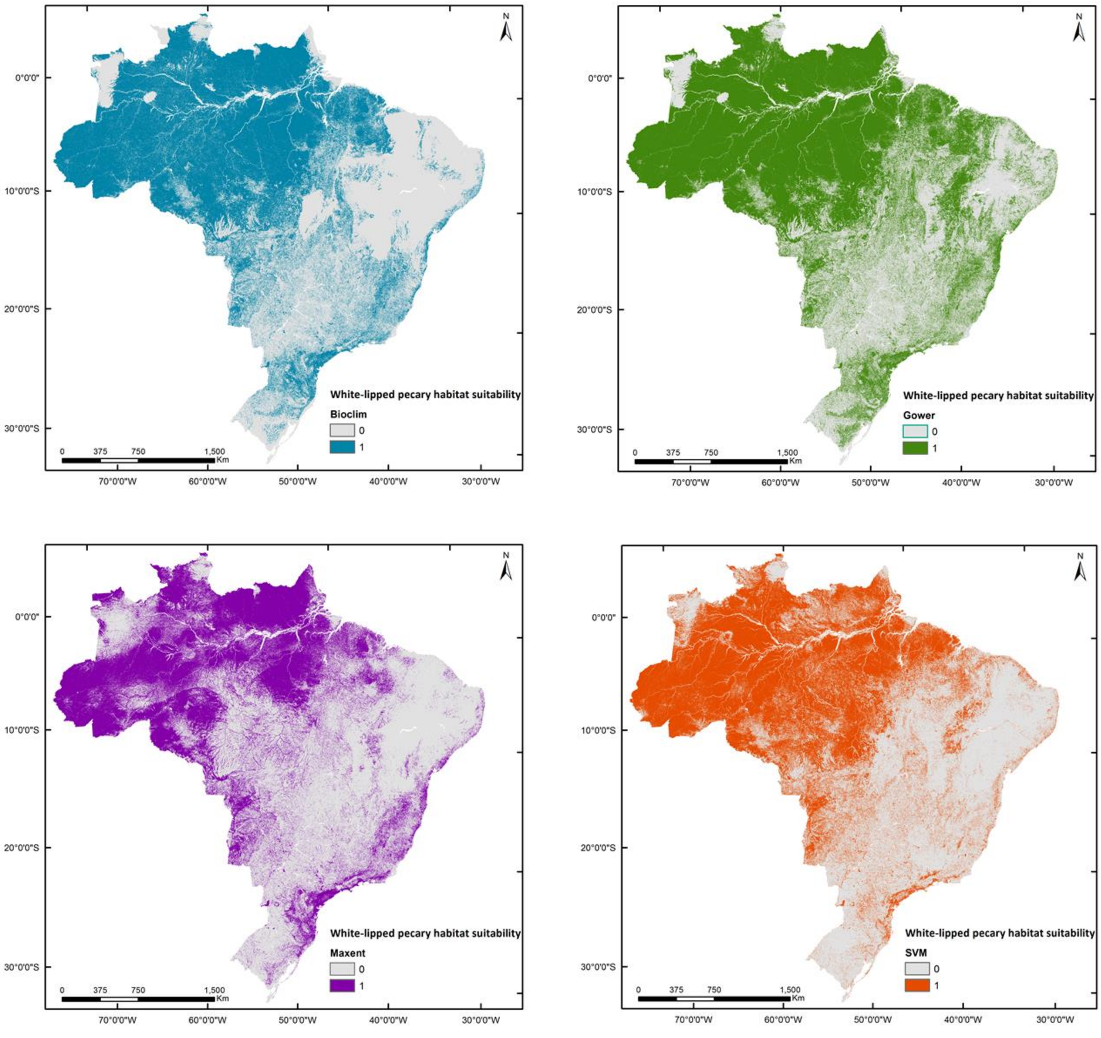
Table SM1. Result tests for Maxent predictions using different model configurations for bias correction: (a) no bias correction, (b) using the kernel density of all occurrence records, (c) using the density of access routes – rivers and paved roads. The same bias corrections were tested but in models including the edge distance variable (a2, b2 and c2). And AUC values were calculated using only linear feature (LF) or the default set with all features (allF).

	AICc	**AICweight**	**AUC LF**	**AUC allF**	**Threshold 95% allF**
(a) Model without distance variable	8631.244	0.916	0.778	0.820	0.161
(b) Model without distance variable with KDE bias correction	8637.045	0.084	0.777	0.807	0.129
(c) Model without distance variable with Access bias correction	8707.840	0.000	0.748	0.791	0.177
(d) Model with forest edge distance	8602.373	0.854	0.791	0.848	0.133
(e) Model with forest edge distance with KDE bias correction	8607.882	0.146	0.795	0.830	0.150
(f) Model with forest edge distance with Access bias correction	8689.989	0.000	0.754	0.811	0.128

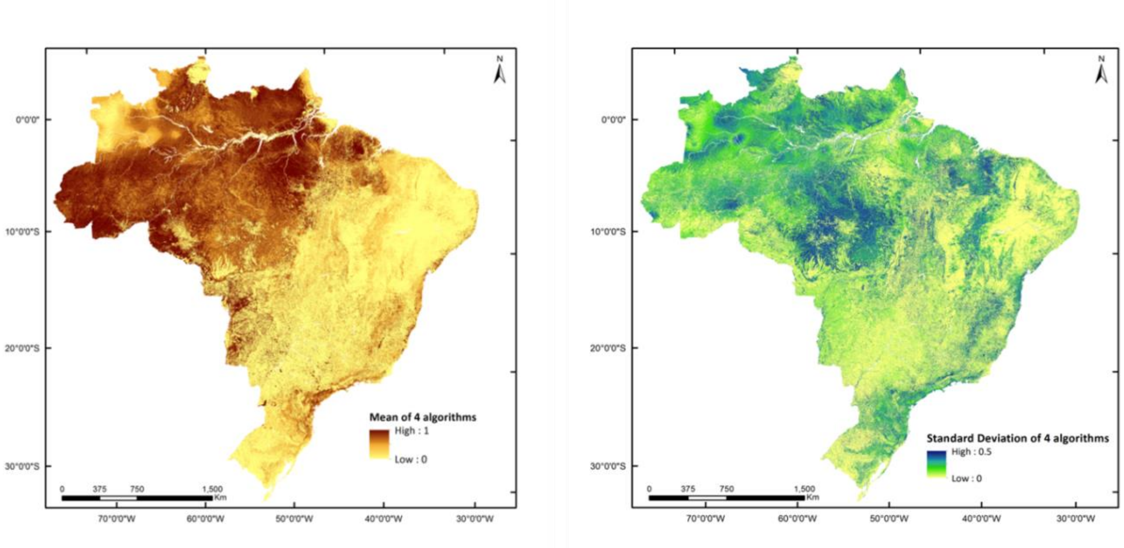
SM3 Model outputs from modeling with (A) and without (B) the forest edge distance variable.



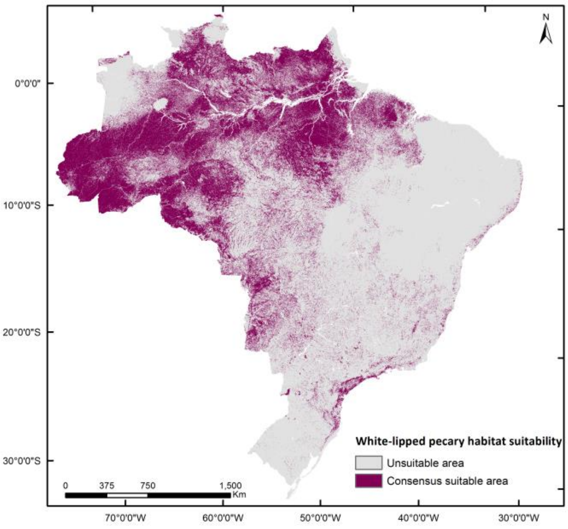
SM4. Model outputs for standard models obtained with Bioclim (blue), Gower distance (green), Maxent (purple) and SVM (orange).



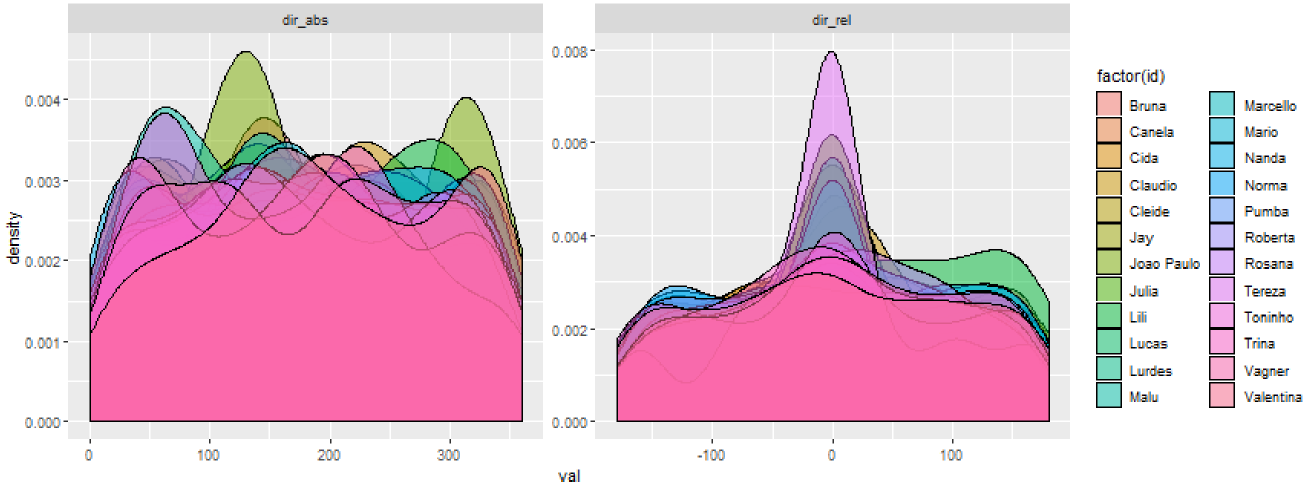
SM5. Model outputs for mean and standard deviation of standard models obtained with the four algorithms tested.



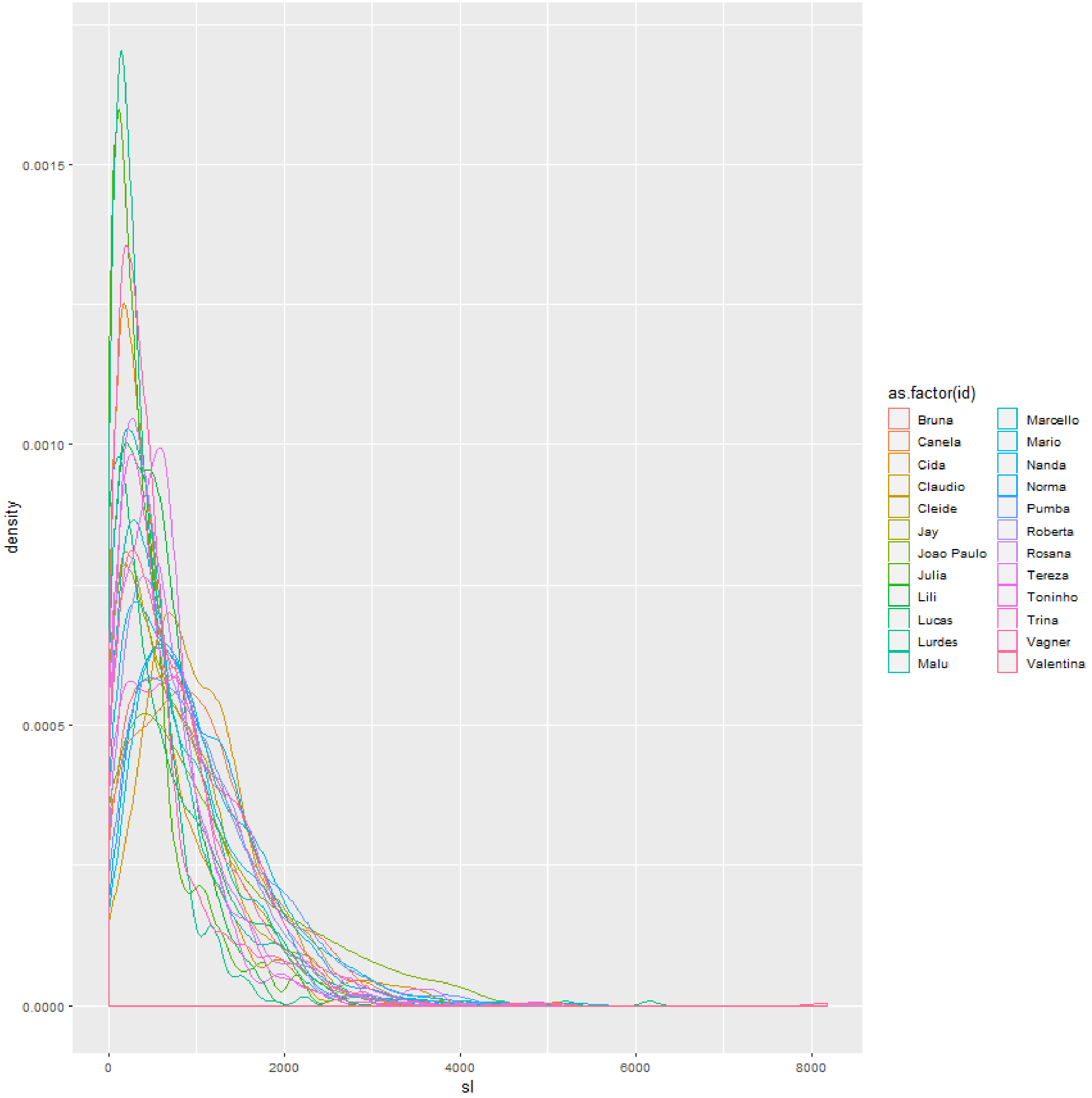
SM6. Consensus area of the 4 algorithms outputs (40 models, 10 per algorithm) for the standard models.



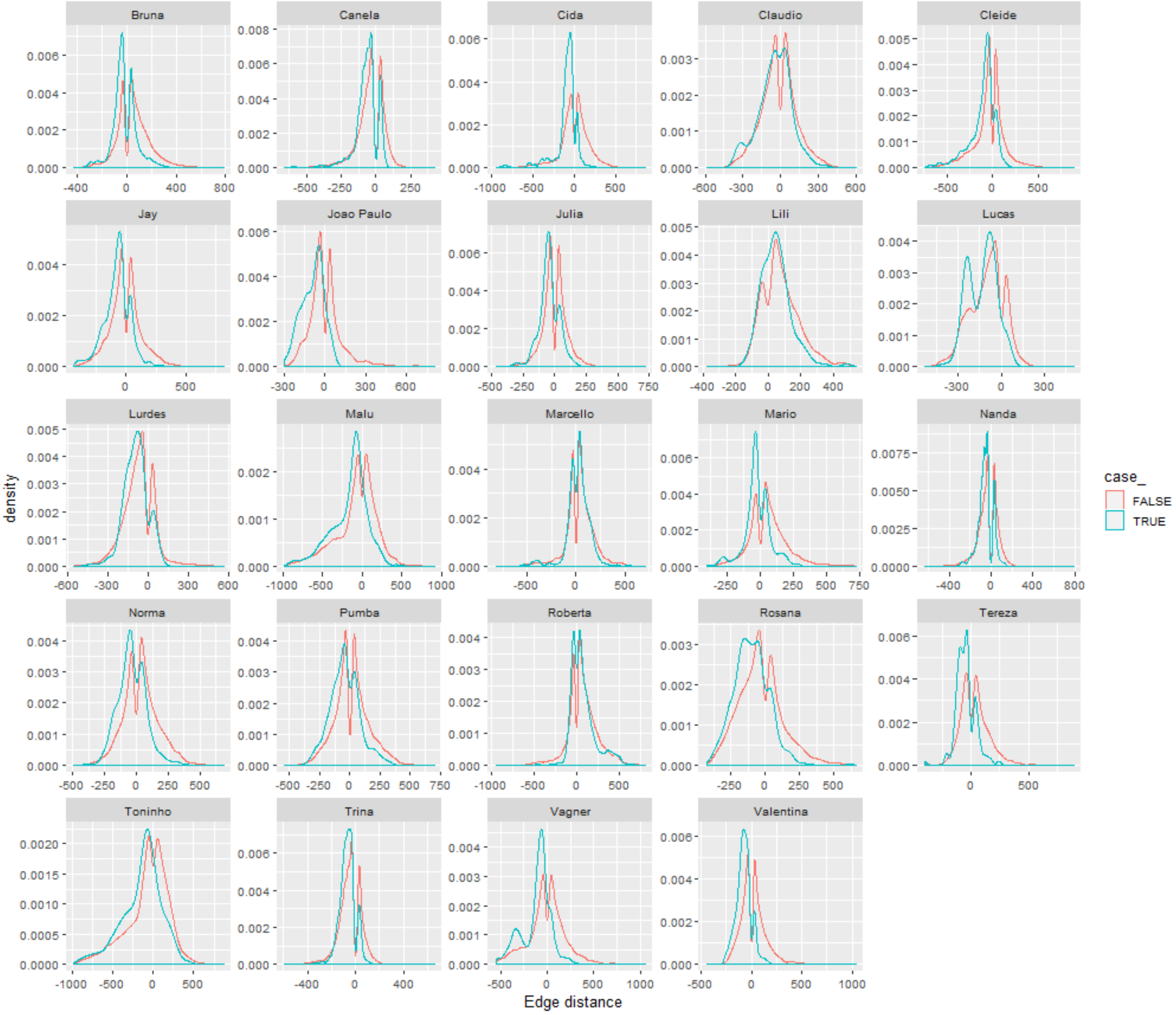
SMC2. SUPPLEMENTARY MATERIAL OF CHAPTER 2



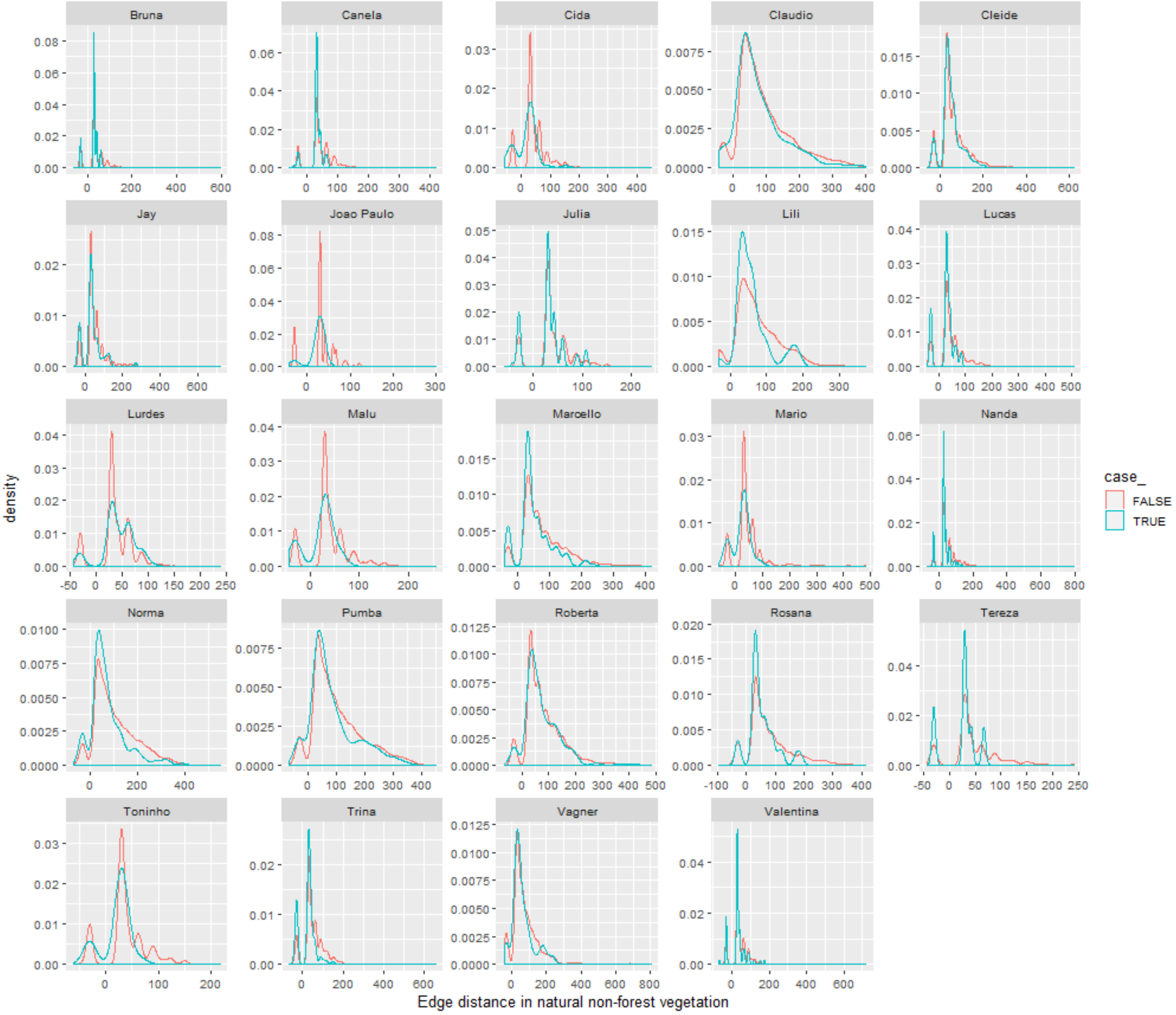
SM1 Absolute and relative turning angles for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



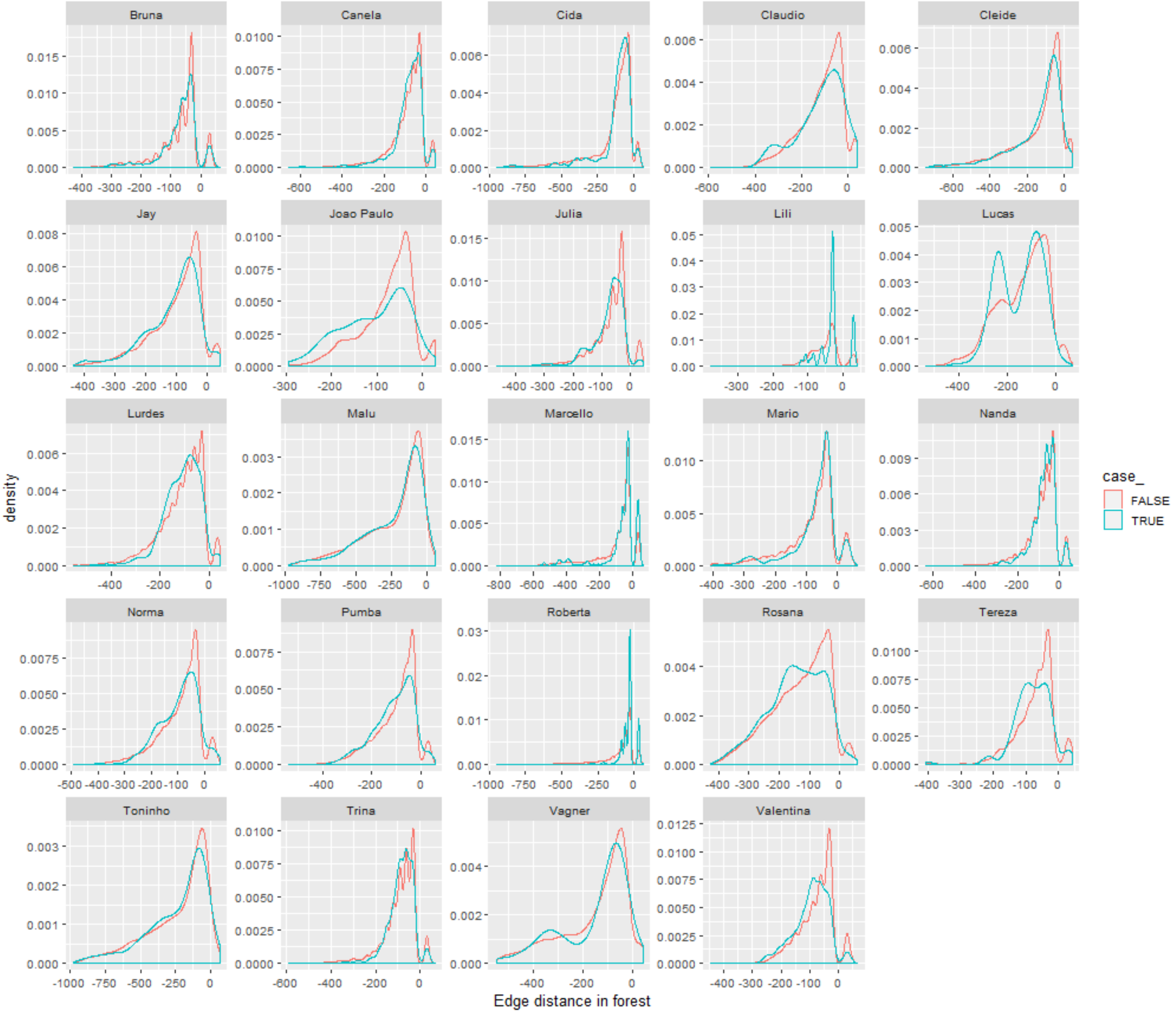
SM2 Step length for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



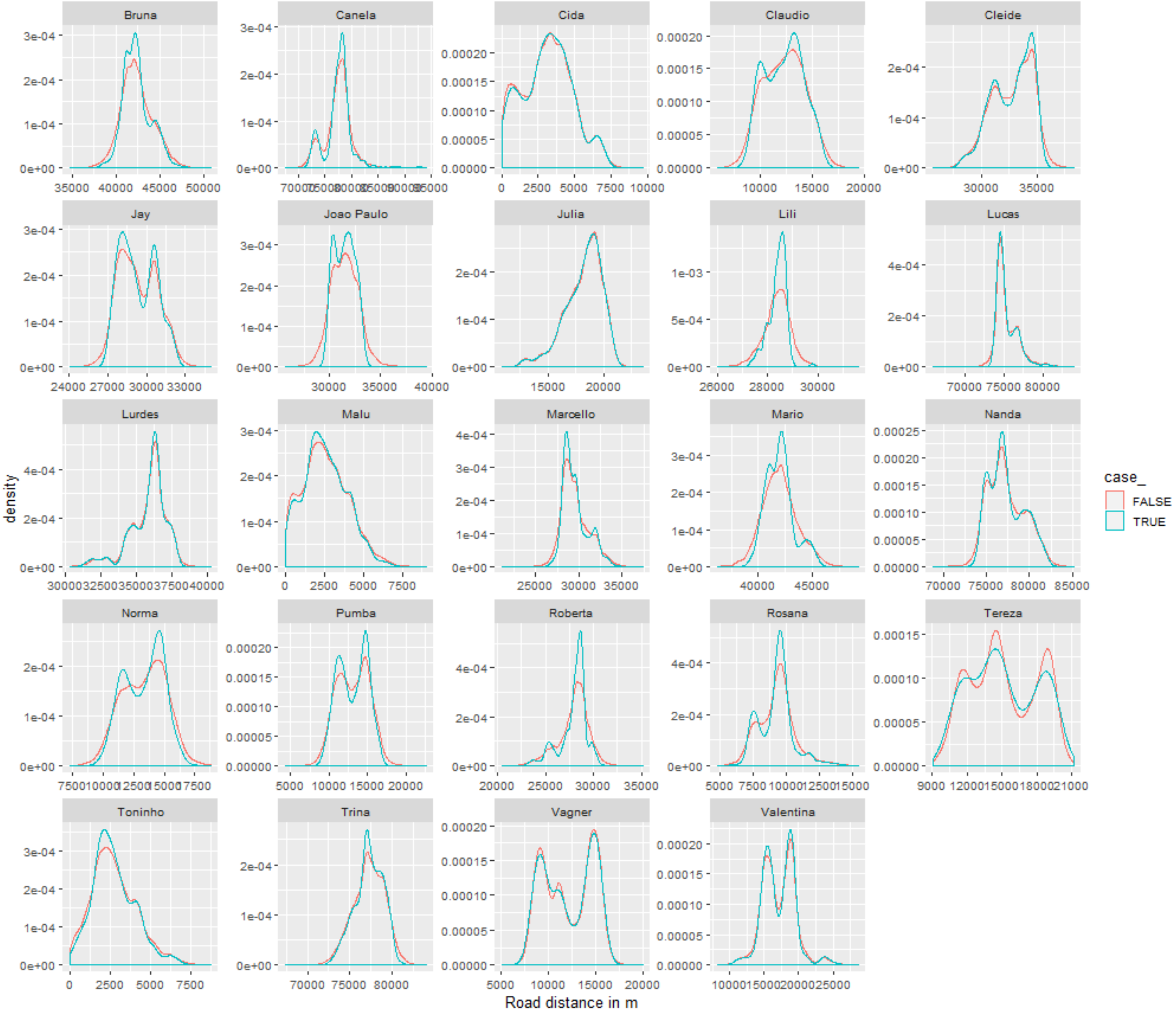
SM3 Forest edge distance (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. The zero mark is forest patch boundary, positive values are the distance in the matrix and the negative values are the distance inside the forest fragment.



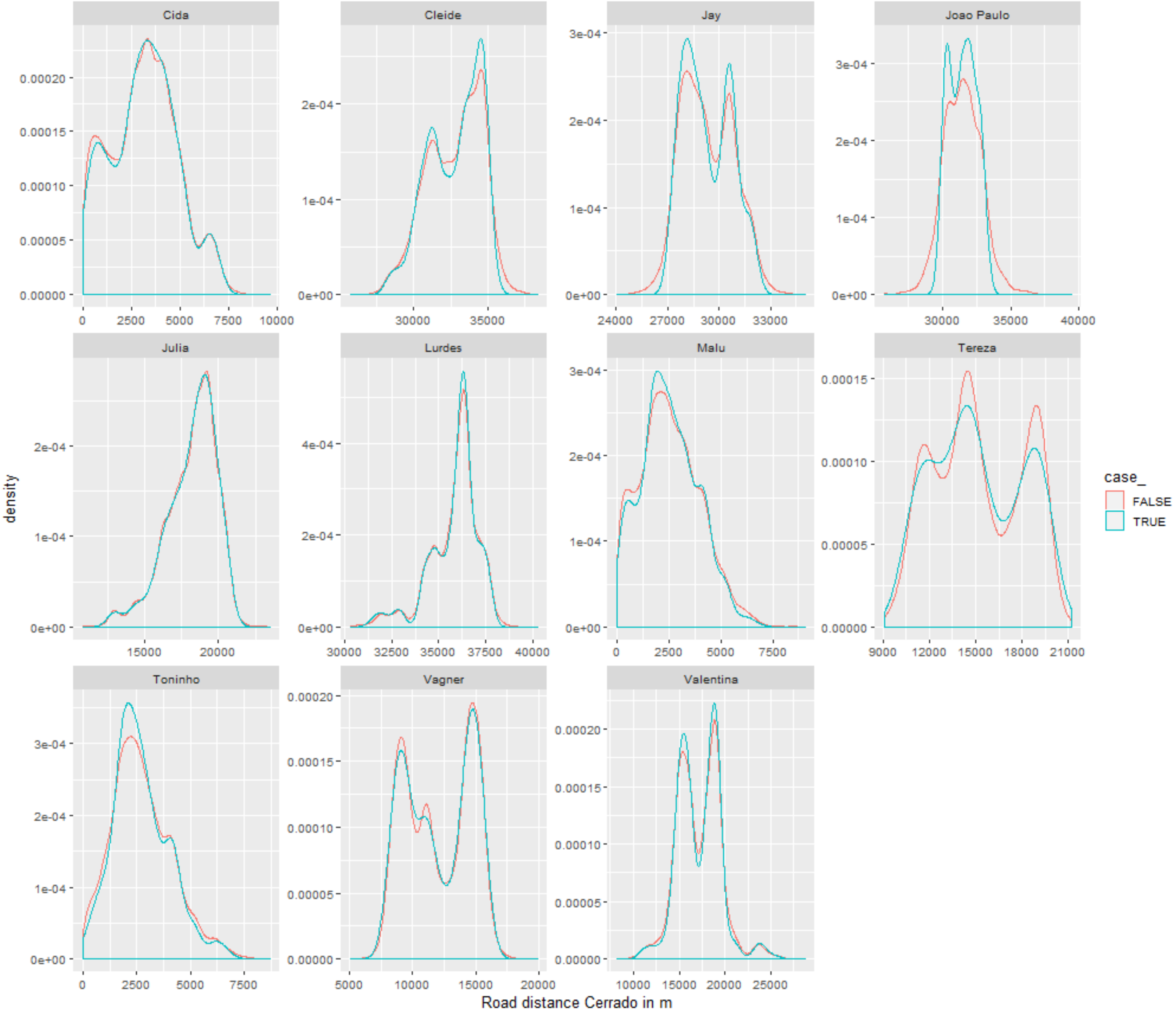
SM4 Edge distance in natural non-forest vegetation (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. The zero mark is forest patch boundary, positive values are the distance in natural non-forest vegetation.



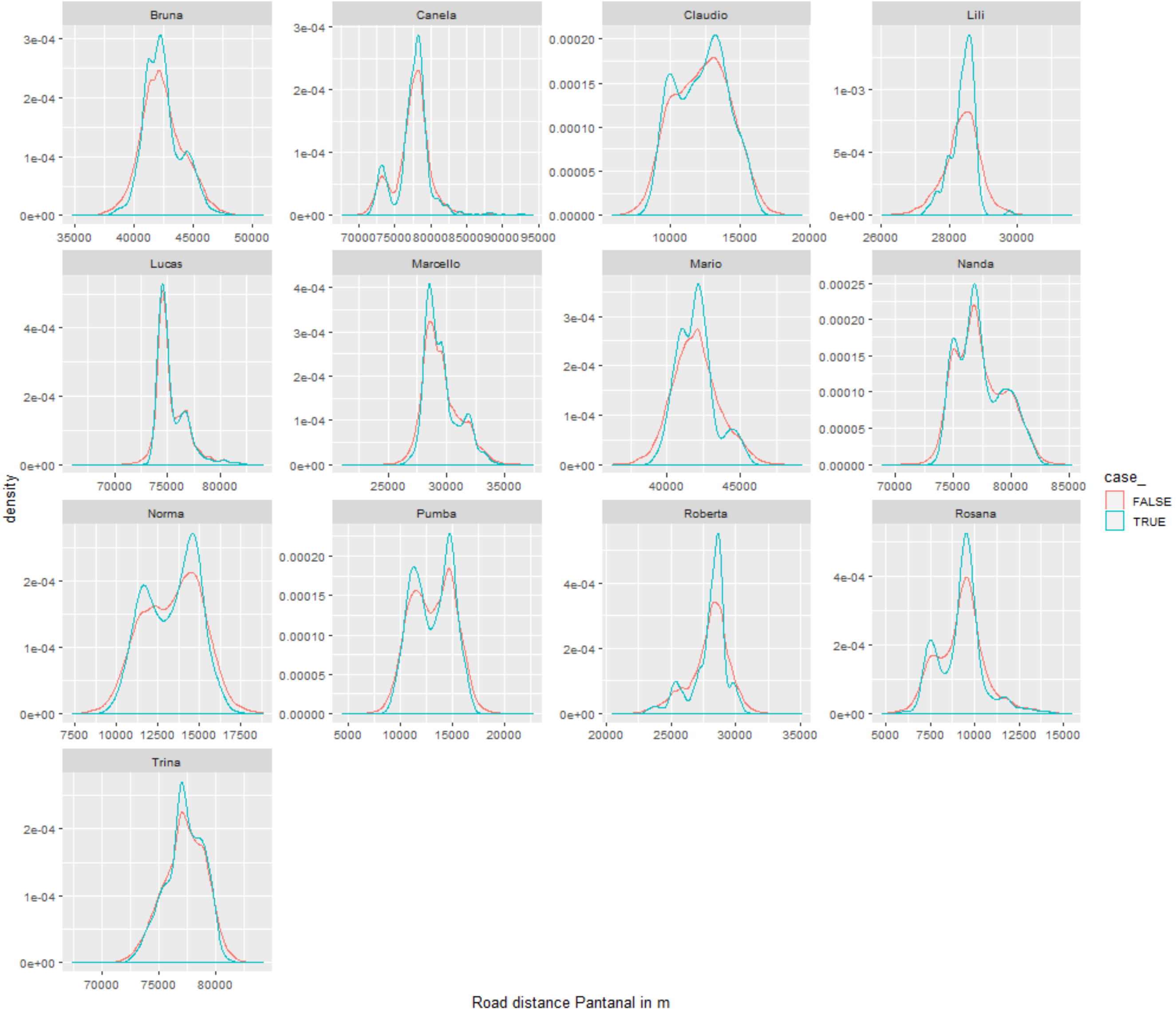
SM5 Forest edge distance inside the forest patch (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. The zero mark is forest patch boundary, and the negative values are the distance inside the forest fragment.



SM6 Paved road distance (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.

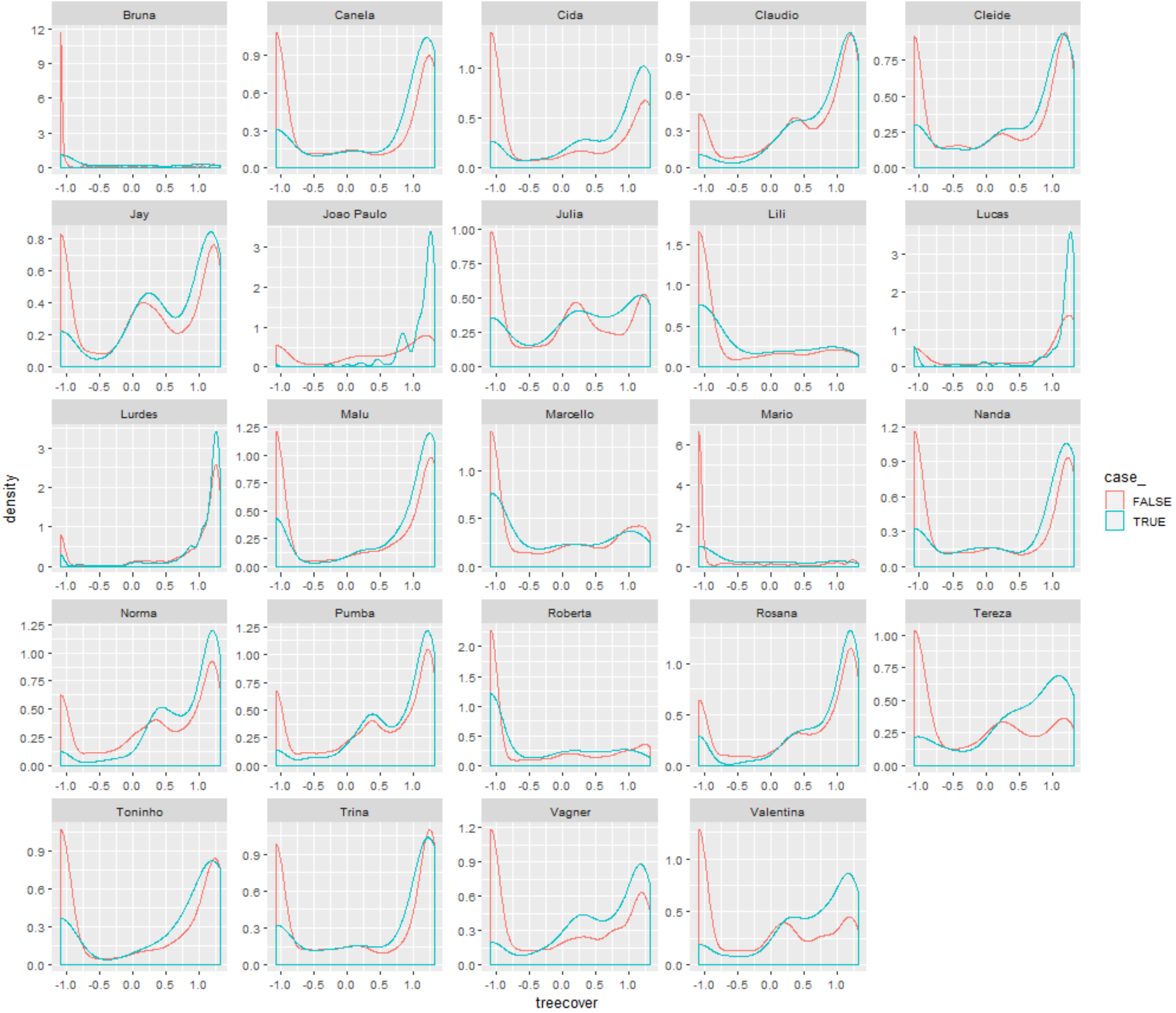


SM7 Paved road distance (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado from Mato Grosso do Sul state, Brazil.

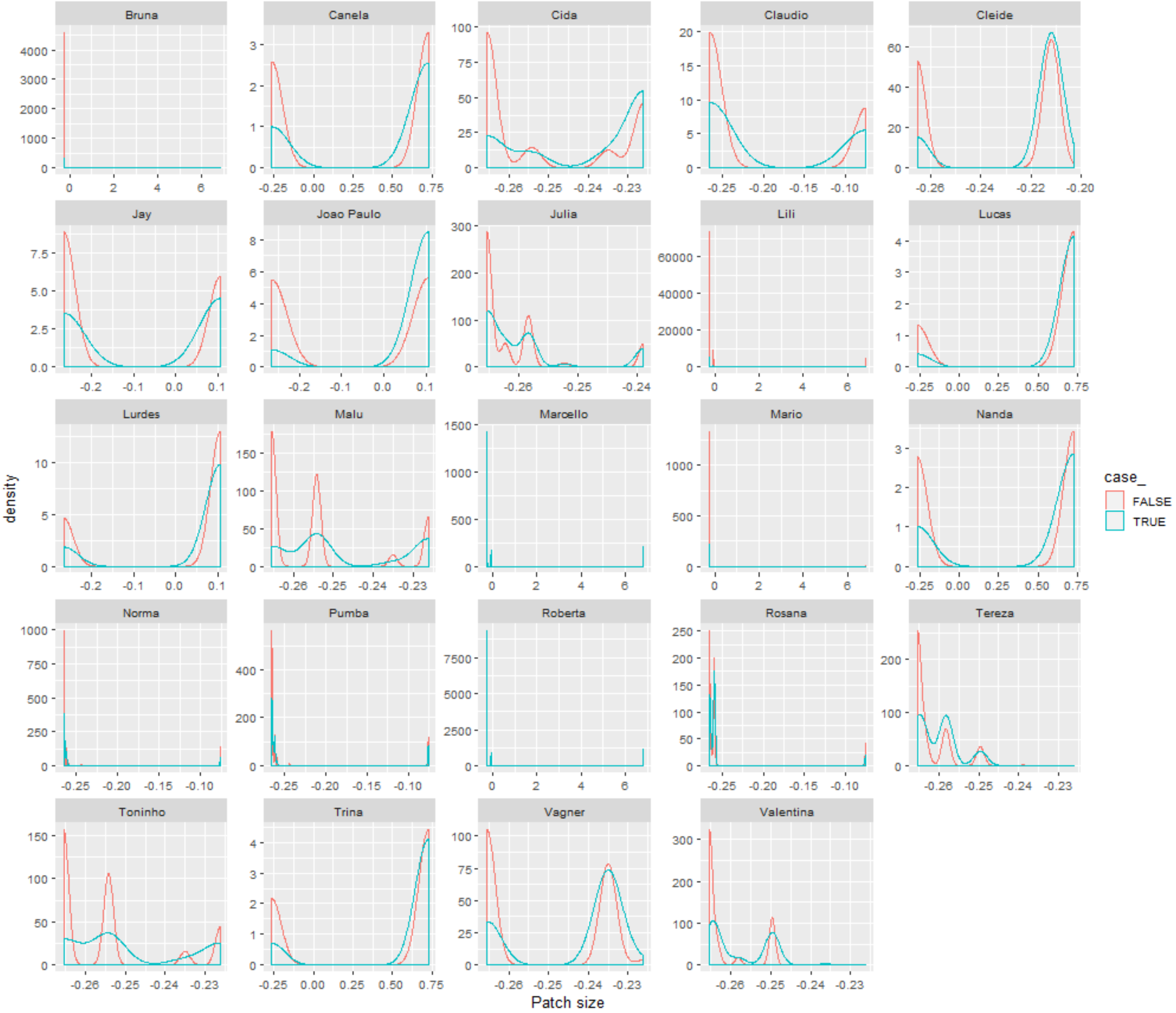


SM8 Paved road distance (in meters) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Pantanal from Mato Grosso do Sul state, Brazil.

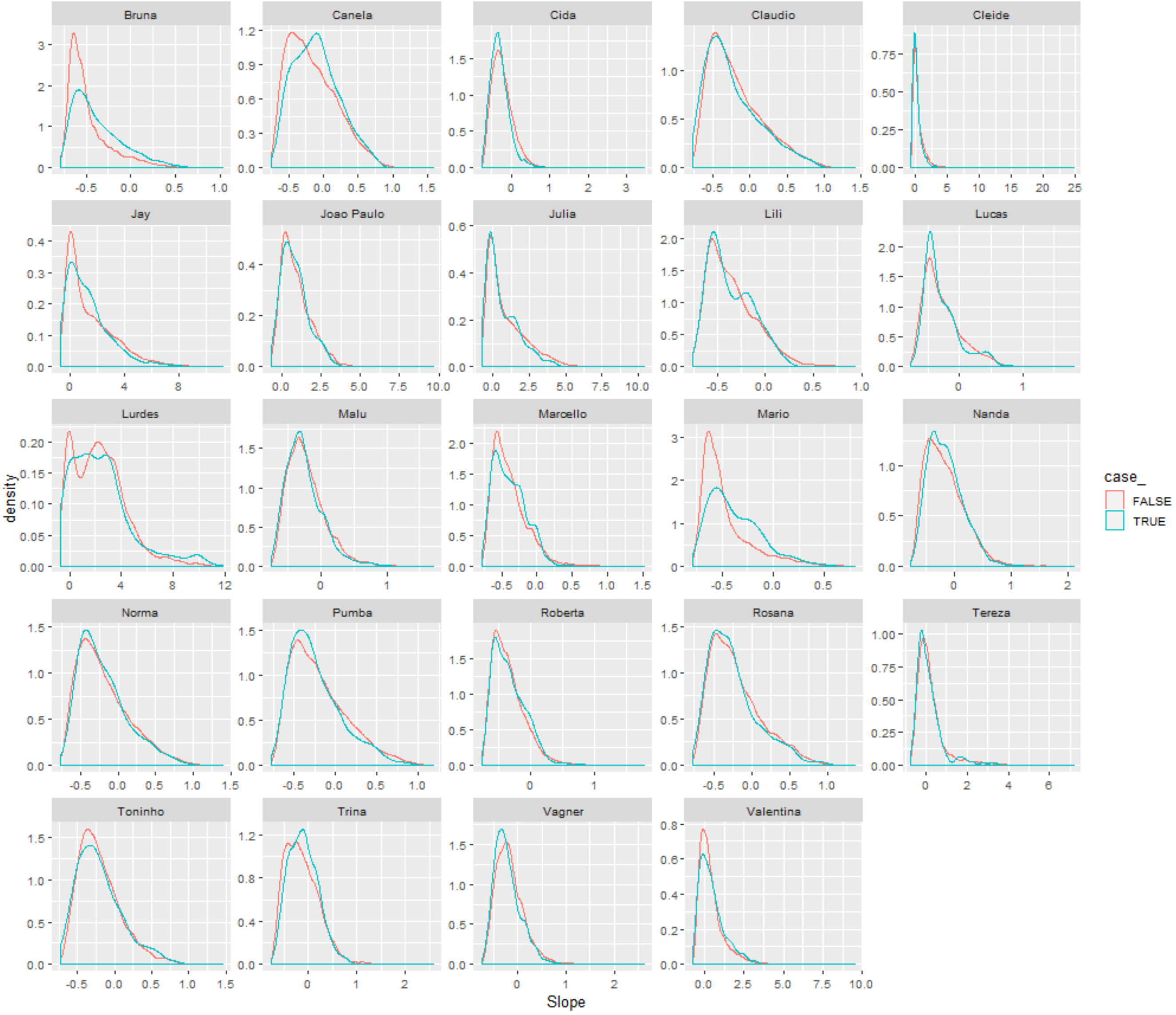
SM9 Landcover associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. Lancover classes tested in the step selection analysis were: (1) matrix mainly composed by pasture, (2) non-forest natural vegetation, and (3) forest vegetation.



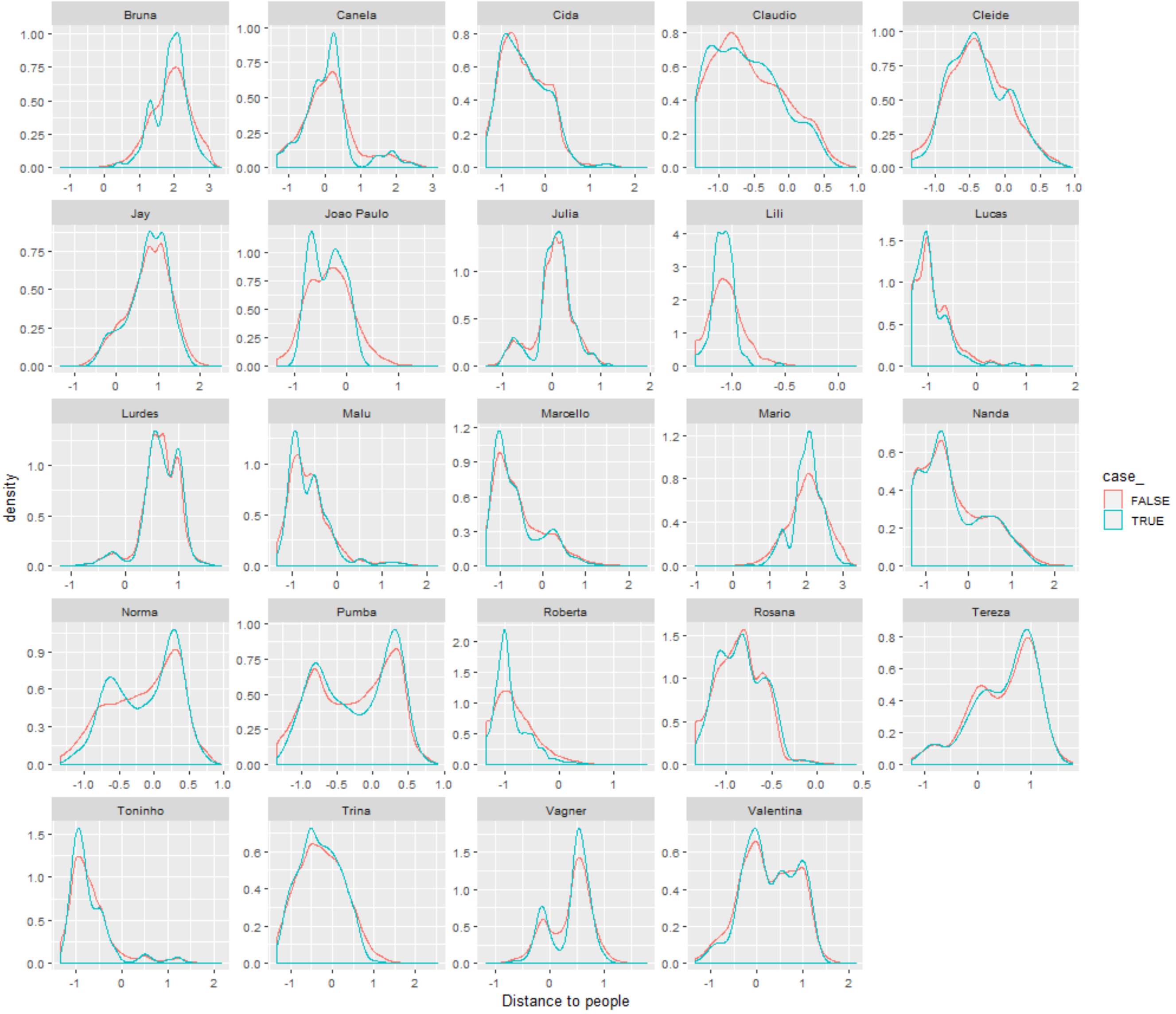
SM10 Percent of tree cover (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored in the Cerrado herds between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



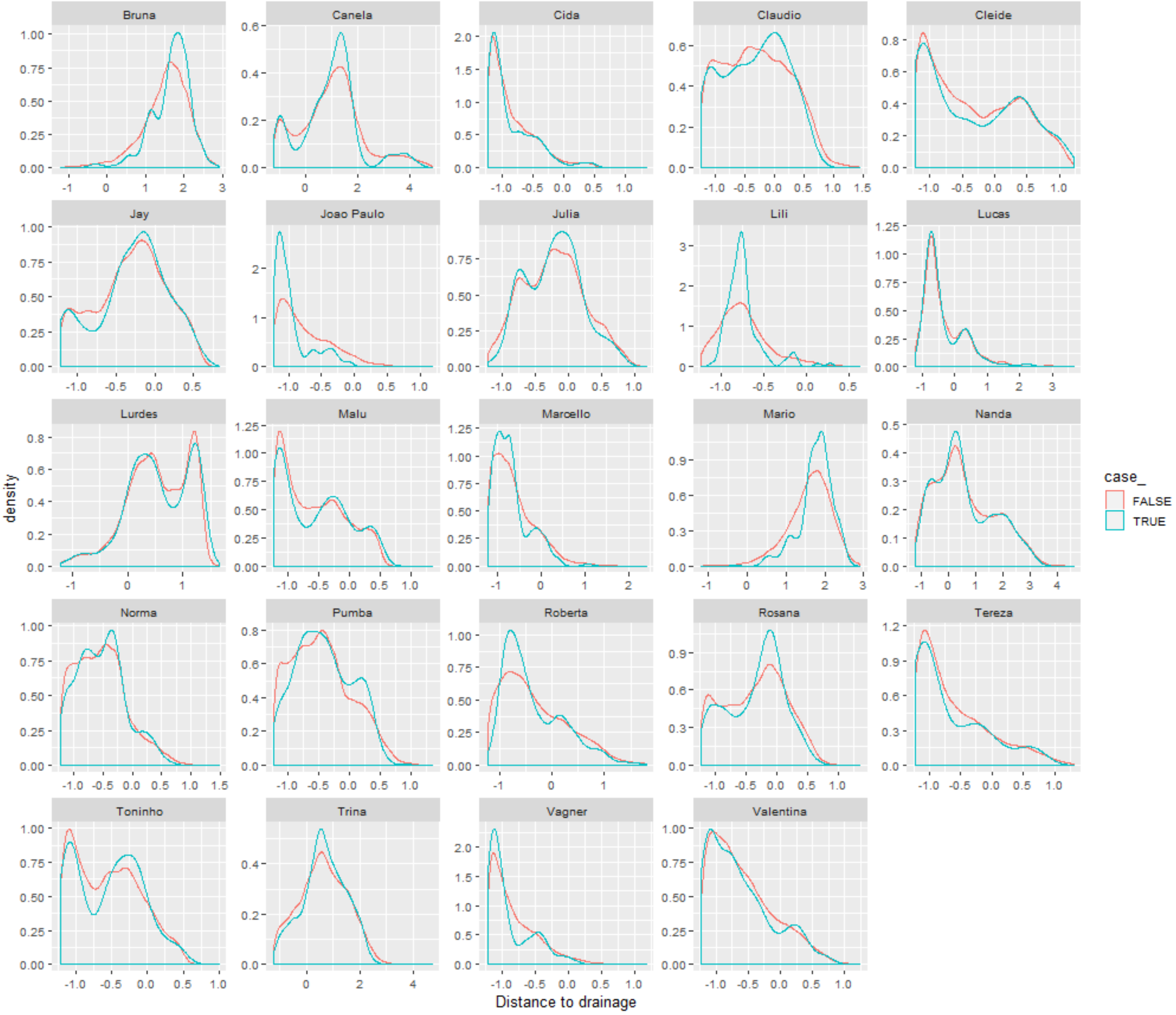
SM11 Forest patch size (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



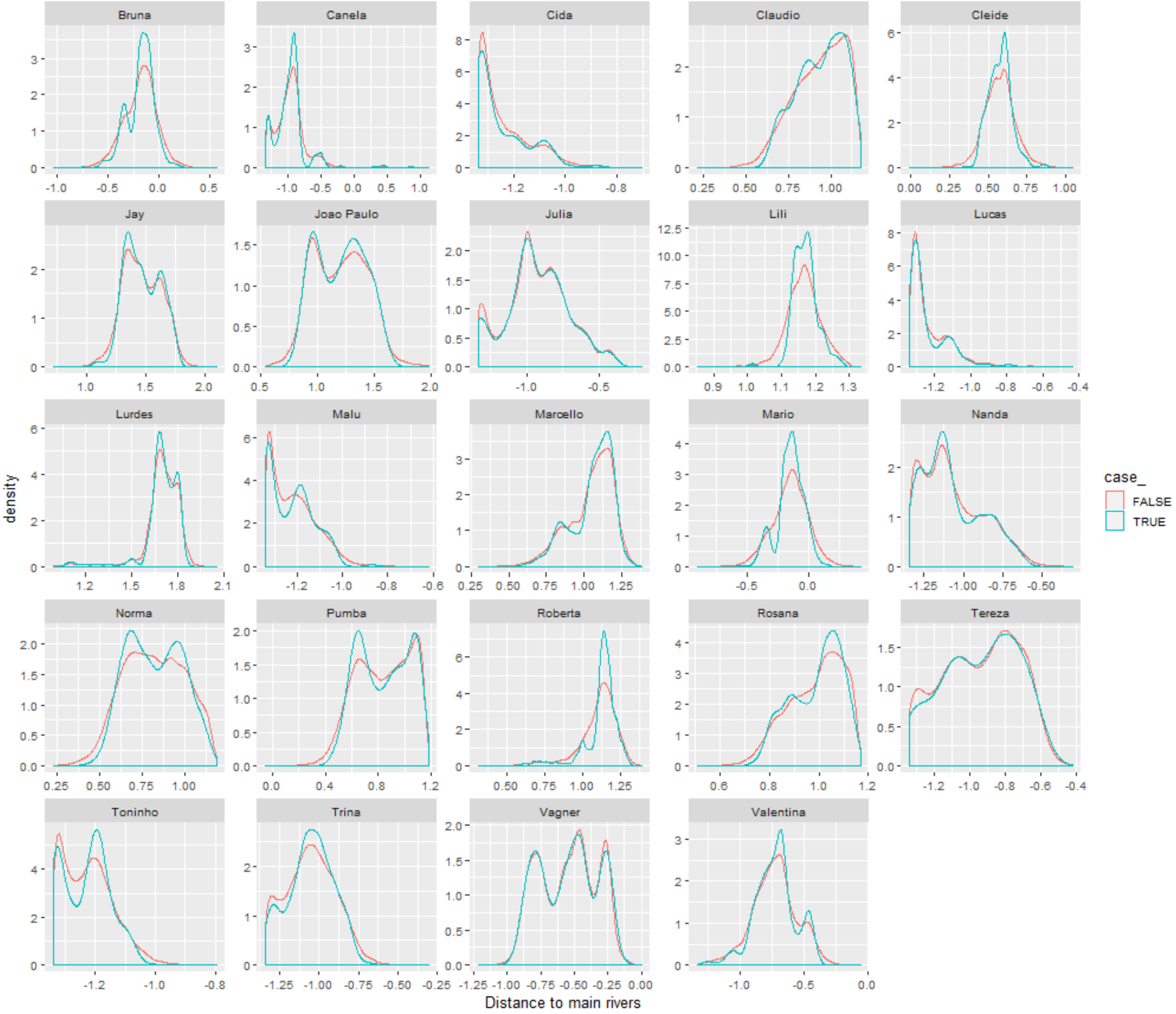
SM12 Slope (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



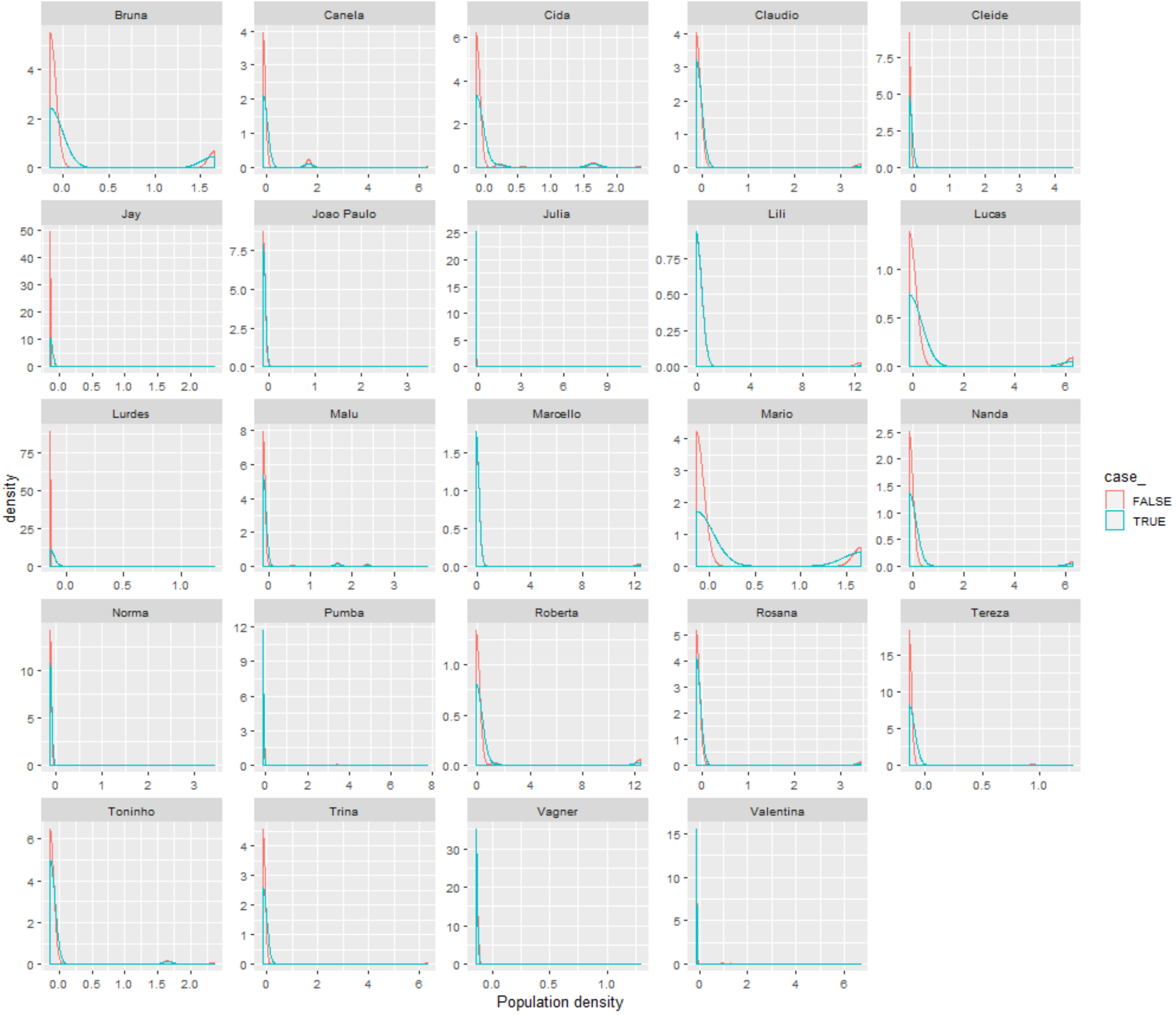
SM13 Distance from human population (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



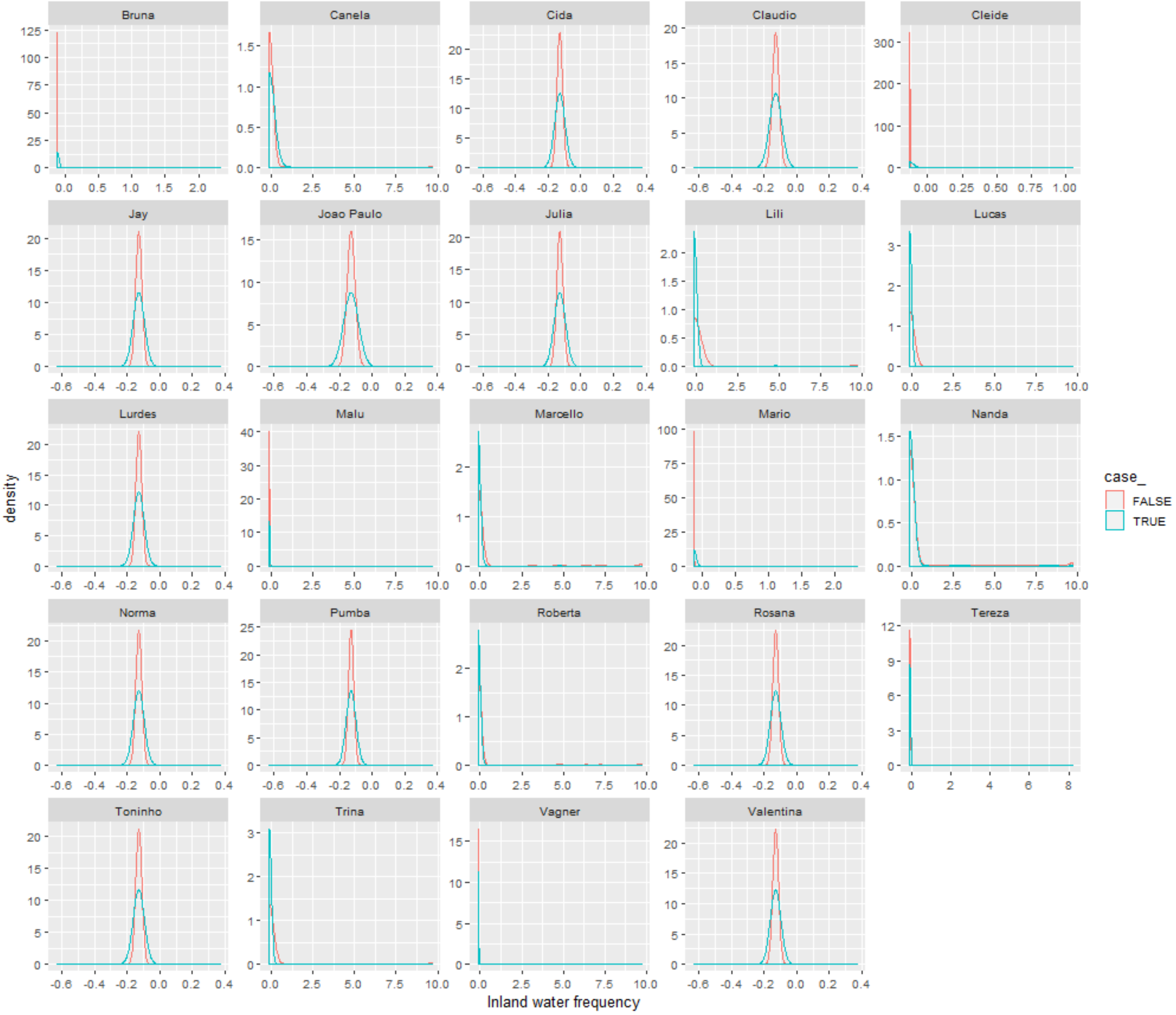
SM14 Distance from drainage (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



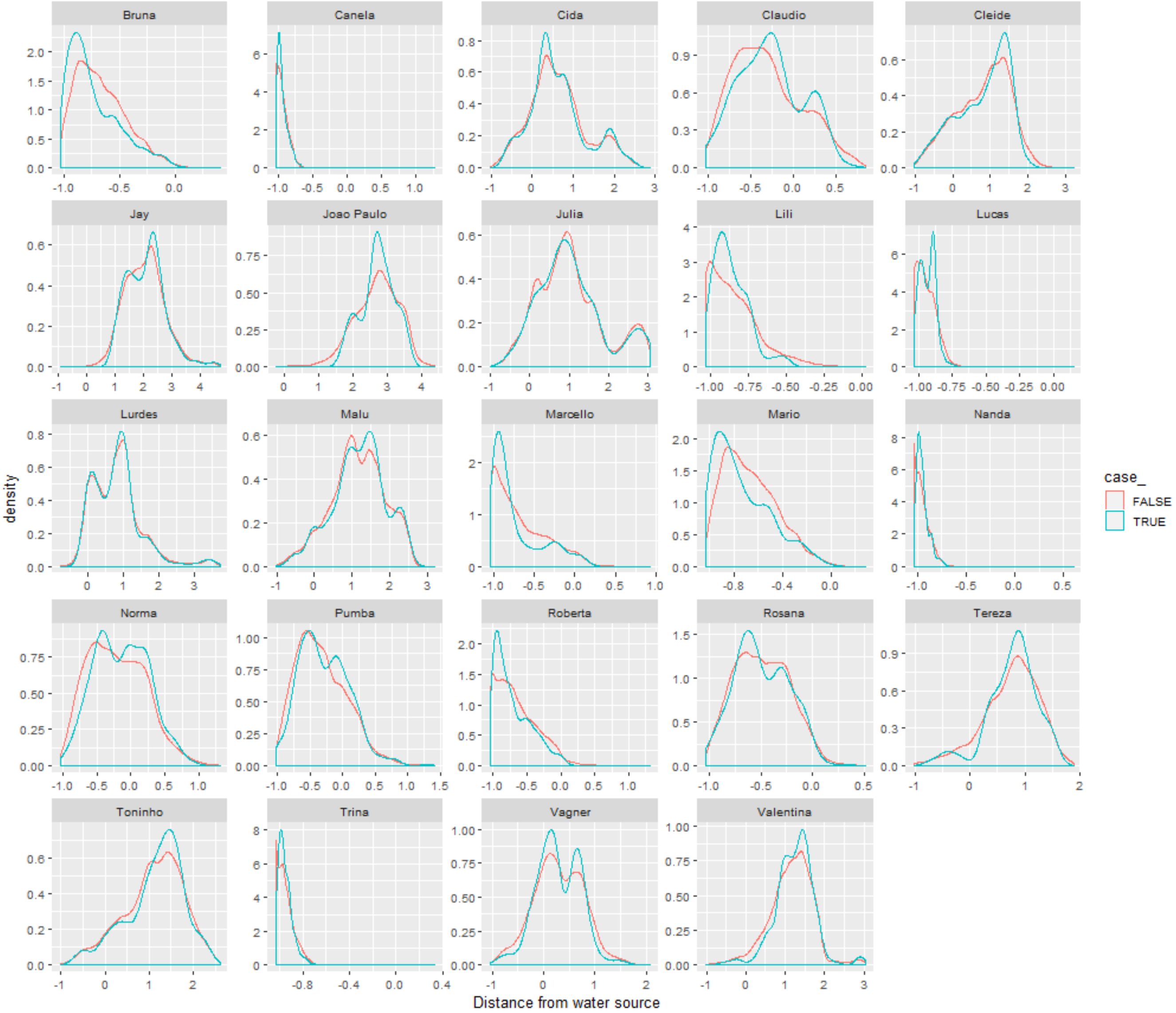
SM15 Distance from main rivers (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



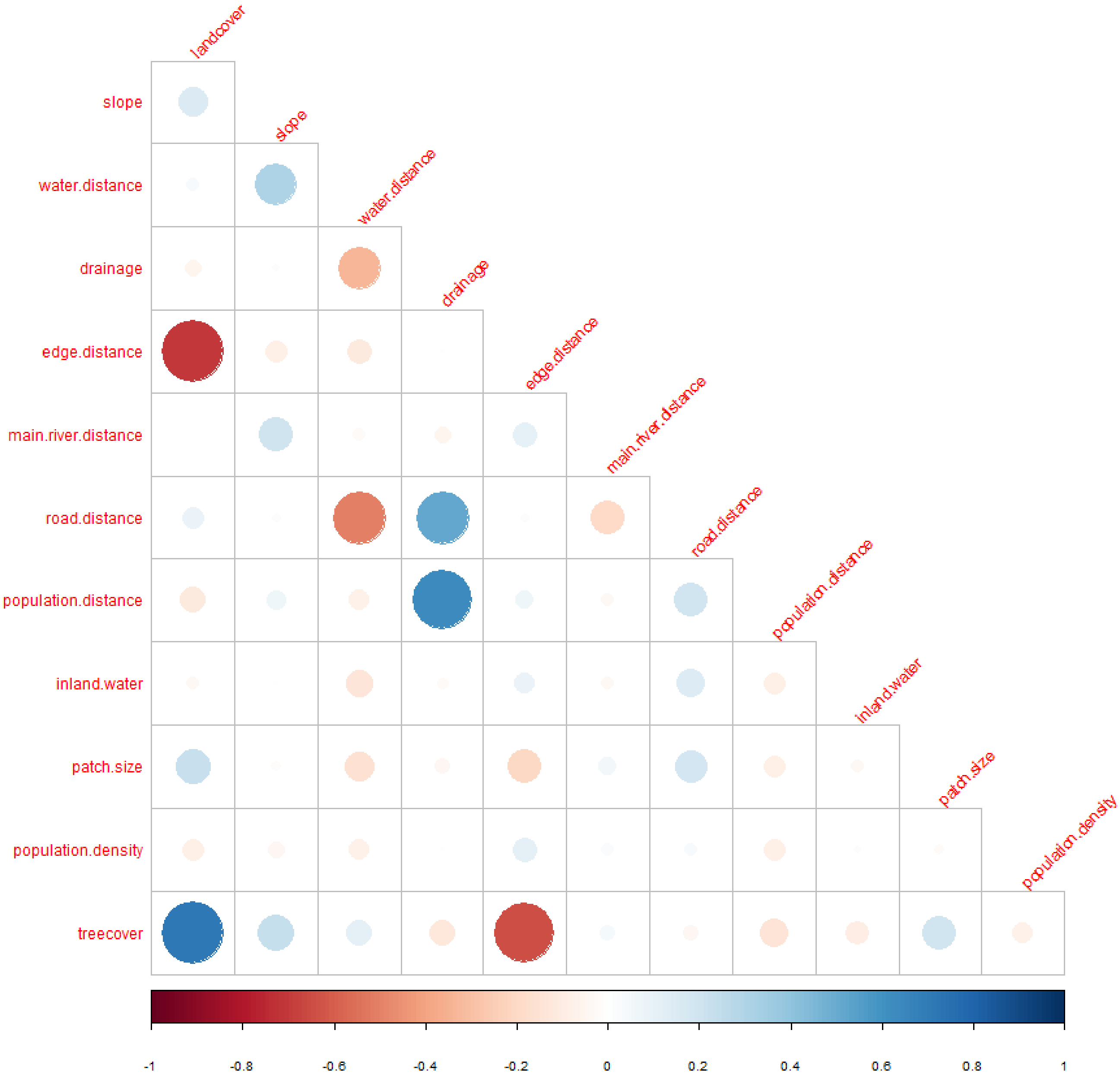
SM16 Population density (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



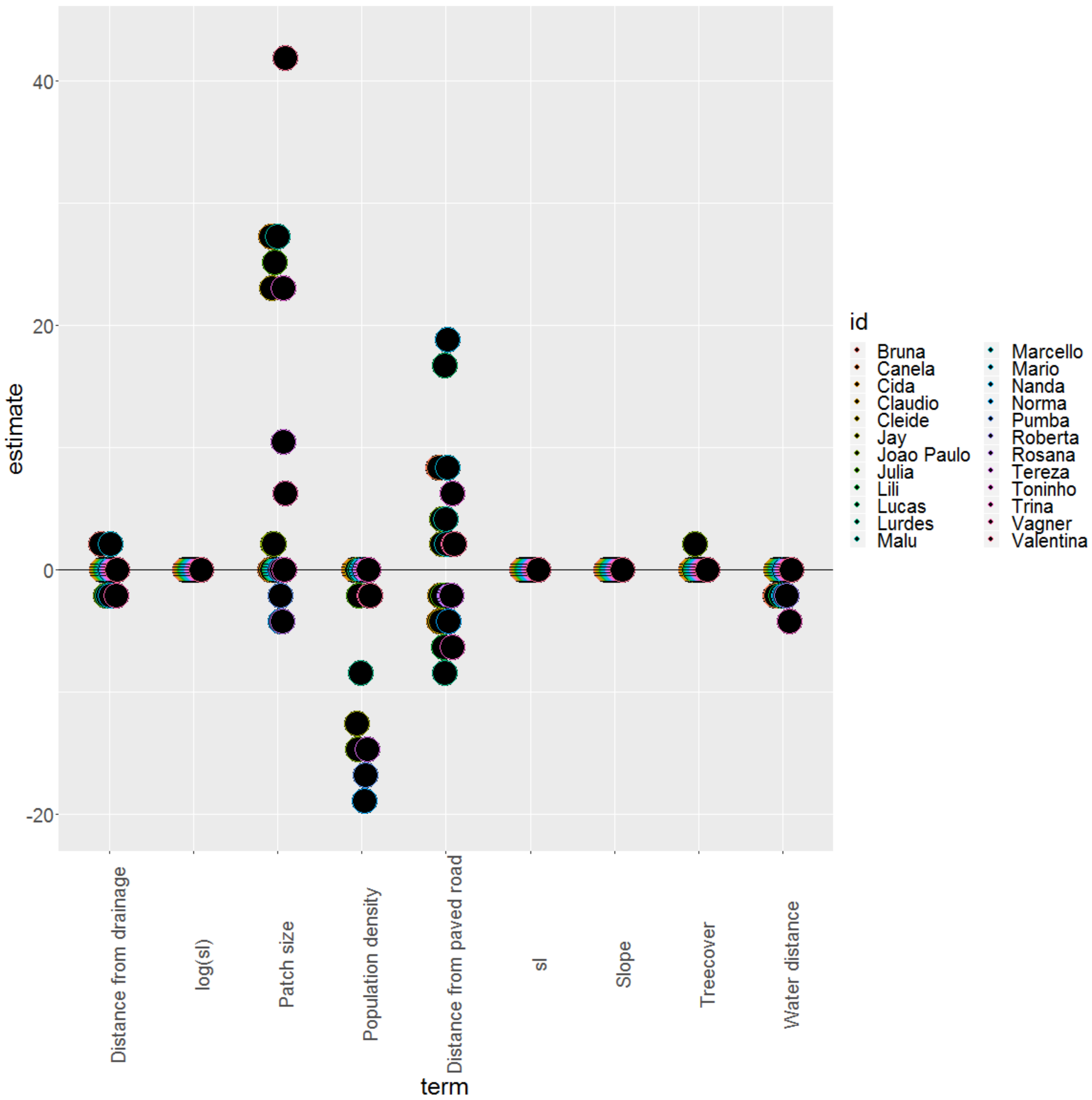
SM17 Inland water frequency (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



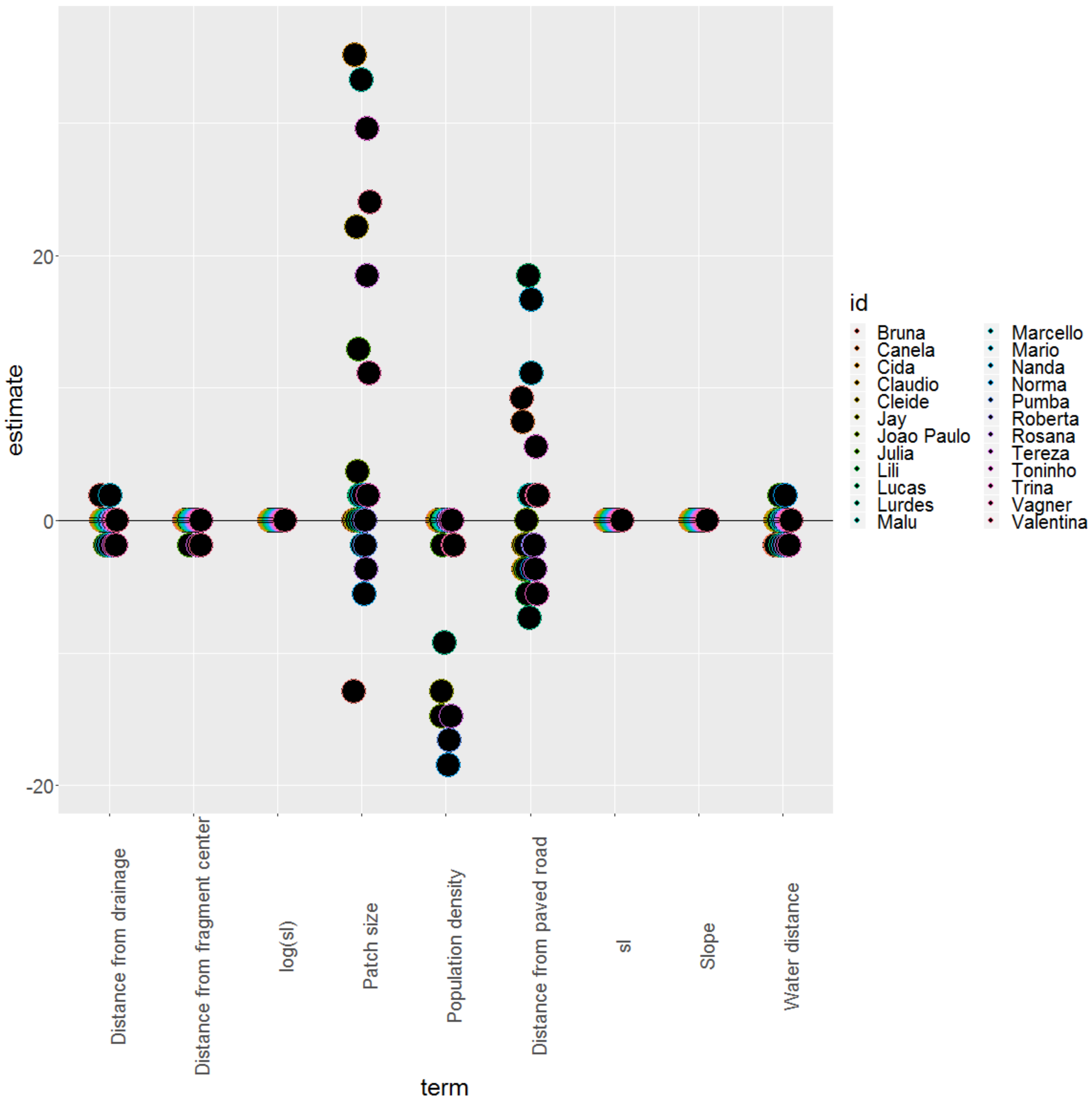
SM18 Distance from water sources (scaled values) associated with used (TRUE case positions) and available (FALSE case positions) steps for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil.



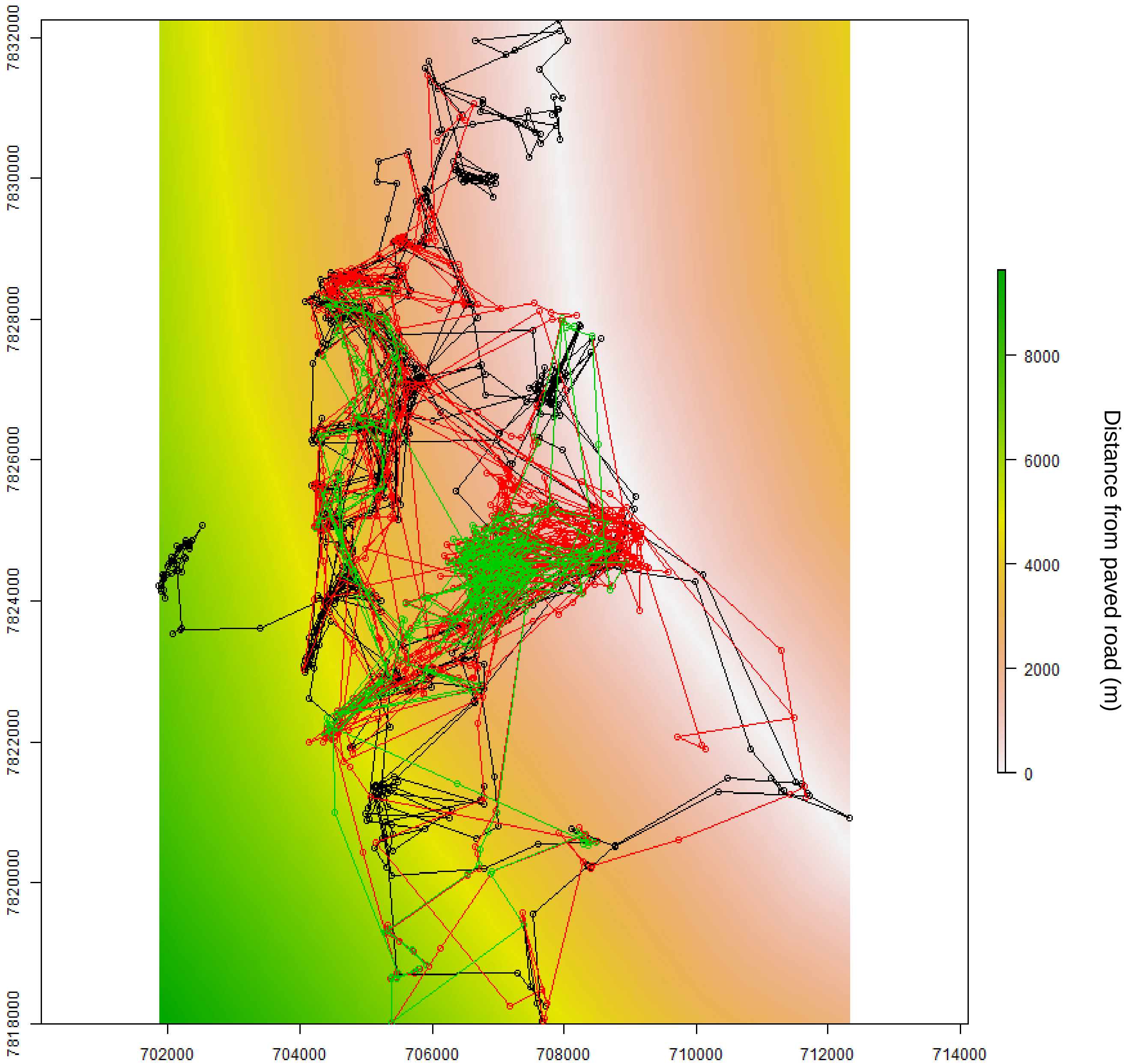
SM19 Results from the Pearson correlation analysis.



SM20 Model 1 results for the Step Selection Function analysis with the two-step approach for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. Dots show the results for estimated coefficients of the twenty-four individual conditional logistic regression models



SM21 Model 2 results for the Step Selection Function analysis with the two-step approach for white-lipped peccaries (*Tayassu pecari)* monitored between 2013 and 2016 in the Cerrado and Pantanal from Mato Grosso do Sul state, Brazil. Dots show the results for estimated coefficients of the twenty-four individual conditional logistic regression models



SM22 GPS tracks for white-lipped peccaries (*Tayassu pecari)* from the Safira herd, monitored between 2013 and 2016 in the Cerrado from Mato Grosso do Sul state, Brazil.

glmm.TMB.random model

```
TMBStruc = glmmTMB(Loc ~
treecover.sc+patch.size.sc+slope.sc+drainage.sc+population.distance.sc+road.distance.sc
            +water.distance.sc+inland.water.sc+(1|step_id) +
             (0 + treecover.sc | ANIMAL_ID) +
             (0 + patch.size.sc | ANIMAL_ID) +
             (0 + slope.sc | ANIMAL_ID)  +
             (0 + drainage.sc | ANIMAL_ID)  +
             (0 + population.distance.sc | ANIMAL_ID)  +
             (0 + road.distance.sc | ANIMAL_ID)  +
             (0 + water.distance.sc | ANIMAL_ID)+
             (0 + inland.water.sc | ANIMAL_ID),
            family=poisson, data=ssfdat, doFit=FALSE)
```

ɫl_vars_glmmherds		**ΑICc**	**lta_AICc**	**odelLik**	**ICcWt**	**LL**	**ım.Wt**
ı.TMB.random	’	;6365.7	0	00E+00	00E+00	8165.8	1
ı.TMB.random.herd1	’	;6558.8	93.1606	14E-42	14E-42	8262.4	1
ı.TMB.random.i2	’	;6842.8	77.1182	48E-104	48E-104	8404.4	1
ı.TMB.random.herd2	.	;7032.6	66.9355	50E-145	50E-145	8505.3	1
ı.TMB.random.herd6	.	;7048.5	82.7968	40E-149	40E-149	8513.2	1
ı.TMB.random.herd3	;	;7133.1	67.3975	30E-167	30E-167	8551.5	1
ı.TMB.random.herd4		;7146.8	81.1578	36E-170	36E-170	8564.4	1
ı.TMB.random.herd5		;7451.2	085.479	96E-236	96E-236	8716.6	1

SM23 Multi-model comparison of step selection function for white-lipped peccary (*Tayassu pecari*) using the Akaike's information Criterion. We compared different generalized linear mixed effect models with individuals and herd as random effects using the Poisson distribution in glmmTMB following Muff et al., 2018.

SMC3. SUPPLEMENTARY MATERIAL OF CHAPTER 3

Table SM1. Adult white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state. Information on study area, sex, period of monitoring and fixes successfully acquired with satellite transmission are presented. Individuals featured in grey were used for the statistical analysis that required regularized data.

Individual	**Biome**	**Area/Herd**	**Sex**	**Start transmission**	**Finish transmission**	**Fixes/ day**	**Total days**	**Total fixes**
Bruna	Pantanal	Caiman 2	F	14-Aug-15	4-Aug-16	8	356	2797
Canela	Pantanal	Barranco Alto	F	28-Jun-15	23-Nov-15	8	148	1165
Cida	Cerrado	Safira	F	18-Dec-15	5-Oct-16	8	292	1293
Claudio	Pantanal	23 de Marco	M	30-Aug-14	14-Nov-14	4	76	275
Cleide	Cerrado	Jacobina	F	9-Mar-15	23-Nov-15	8	259	1760
Dan	Cerrado	Colorado	M	22-Jun-16	26-Oct-16	8	126	73
Ge	Pantanal	Barranco Alto	M	27-Jun-16	16-Dec-16	8 and 6	172	908
Jay	Cerrado	Colorado	M	11-Jul-13	28-Oct-13	4	109	380
Joao Paulo	Cerrado	Colorado	M	21-Feb-15	30-Mar-15	24 and 12	37	310
Julia	Cerrado	Claudia	F	28-Jul-14	6-Dec-14	4	131	349
Lili	Pantanal	Caiman 1	F	3-Dec-14	3-Jan-15	4	31	113
Lucas	Pantanal	Barranco Alto	M	1-Jun-15	27-Jul-15	8	56	457
Lurdes	Cerrado	Colorado	F	5-Jun-14	17-Jan-15	4	226	462
Malu	Cerrado	Safira	F	8-Jun-14	11-Dec-14	4	186	504
Malu II	Cerrado	Safira	F	30-Sep-15	7-Mar-16	8	159	733
Marcello	Pantanal	Caiman 1	M	15-Aug-15	5-Mar-16	8	203	1246
Marcos	Cerrado	Taboco	M	18-Feb-16	29-Apr-16	8	71	40
Mario	Pantanal	Caiman 2	M	14-Aug-15	17-Mar-16	8	216	990
Nalva	Cerrado	Claudia	F	27-Jul-14	2-Sep-14	4	37	60
Nanda	Pantanal	Barranco Alto	F	24-Jun-15	13-Jan-16	8	203	1584
Norma	Pantanal	23 de Marco	F	31-Aug-14	1-Feb-15	4	154	507
Pumba	Pantanal	23 de Marco	F	20-Apr-15	4-Jan-16	8	259	1800
Roberta	Pantanal	Caiman 1	F	16-Aug-15	21-Aug-16	8	371	2935
Rosana	Pantanal	23 de Marco	F	24-Nov-15	21-Jul-16	8	240	1240
Simao	Pantanal	23 de Marco	M	20-Apr-15	8-Jul-15	8	79	138
Tainara	Cerrado	Jacobina	F	9-Mar-15	20-Jan-16	8 and 6	317	1644
Tereza	Cerrado	Santa Tereza	F	6-Mar-15	24-May-15	4	79	110
Toninho	Cerrado	Safira	M	8-Jun-14	25-Nov-14	4	170	397
Trina	Pantanal	Barranco Alto	F	26-Jun-15	3-Mar-16	8	251	1598

Vagner	Cerrado	Taboco	M	18-Feb-16	11-Aug-16	8	175	1151
Valentina	Cerrado	Santa Tereza	F	9-Aug-15	7-Mar-16	8	211	1167

Table SM2. Multimodel inference for daily displacement and median speed of adult white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. We present results for generalized linear models and non-linear mixed effect models with random intercept for Biome.

Multimodel inference for daily displacement and median speed				
Daily distance - glm				
Models	**AICc**	**dAICc**	**df**	**weight**
Biome + Time Tracked	-23.9	0.0	4	0.82
Biome + Time Tracked + Sex	-20.8	3.1	5	0.18
Biome + Time Tracked + Herd	9.8	33.7	12	<0.001
Biome + Time Tracked + Sex + Herd	18.3	42.2	13	<0.001
Median Speed - glm				
Models	**AICc**	**dAICc**	**df**	**weight**
Biome + Time Tracked	-20.4	0.0	4	0.79
Biome + Time Tracked + Sex	-17.7	2.7	5	0.21
Biome + Time Tracked + Herd	8.7	29.1	12	<0.001
Biome + Time Tracked + Sex + Herd	16.5	36.9	13	<0.001
Log 10 Daily distance with mean landscape variables glm				
Models	**AICc**	**dAICc**	**df**	**weight**
Biome + Time Tracked	-22.00	0.0	4	0.4984
Biome + Time Tracked + Slope	-20.50	1.4	5	0.2427
Biome + Time Tracked + Slope + Tree cover	-19.80	2.1	6	0.1702
Biome + Time Tracked + Slope + Patch size	-17.70	4.3	6	0.0577
Biome + Time Tracked + Slope + Edge distance + Patch size + Tree cover	-15.90	6.1	8	0.0233
Biome + Time Tracked + Slope + Edge distance + Patch size	-13.60	8.4	7	0.0076
Log 10 Median Speed with mean landscape variables glm				
Models	**AICc**	**dAICc**	**df**	**weight**
Biome + Time Tracked + Slope + Patch size	-153.3	0.0	6	0.5614
Biome + Time Tracked + Slope + Edge distance + Patch size + Treecover	-152.4	0.9	8	0.361

Biome + Time Tracked + Slope + Edge distance + Patch size	-149.3	4.0	7	0.0749
Biome + Time Tracked	-142.6	10.7	4	0.0027
Biome + Time Tracked + Slope + Tree cover	-131.9	21.4	6	<0.001
Biome + Time Tracked + Slope	-130	23.3	5	<0.001

Log 10 Daily distance with mean landscape variables mixed effect model with random intercept to Biome - population effect

Models	AICc	dAICc	df	weight
random intercept (Biome) + Time Tracked	0.2	0.0	4	0.9884
random intercept (Biome) + Time Tracked + Slope	9.4	9.2	5	0.01
random intercept (Biome) + Time Tracked + Tree cover	13.5	13.3	5	0.0013
random intercept (Biome) + Time Tracked + Edge distance	16.5	16.3	5	<0.001
random intercept (Biome) + Time Tracked + Slope + Tree cover	21.8	21.6	6	<0.001
random intercept (Biome) + Time Tracked + Population distance	23.8	23.6	5	<0.001
random intercept (Biome) + Time Tracked + Patch size	28	27.8	5	<0.001
random intercept (Biome) + Time Tracked + Road distance	28.7	28.6	5	<0.001
random intercept (Biome) + Time Tracked + Slope + Patch size	38.2	38.1	6	<0.001
random intercept (Biome) + Time Tracked + Slope + Edge distance + Patch size	55.3	55.1	7	<0.001
random intercept (Biome) + Time Tracked + Slope + Edge distance + Patch size + Treecover	57	56.8	7	<0.001

Log 10 Median Speed with mean landscape variables mixed effect model with random slope to Biome - population effect

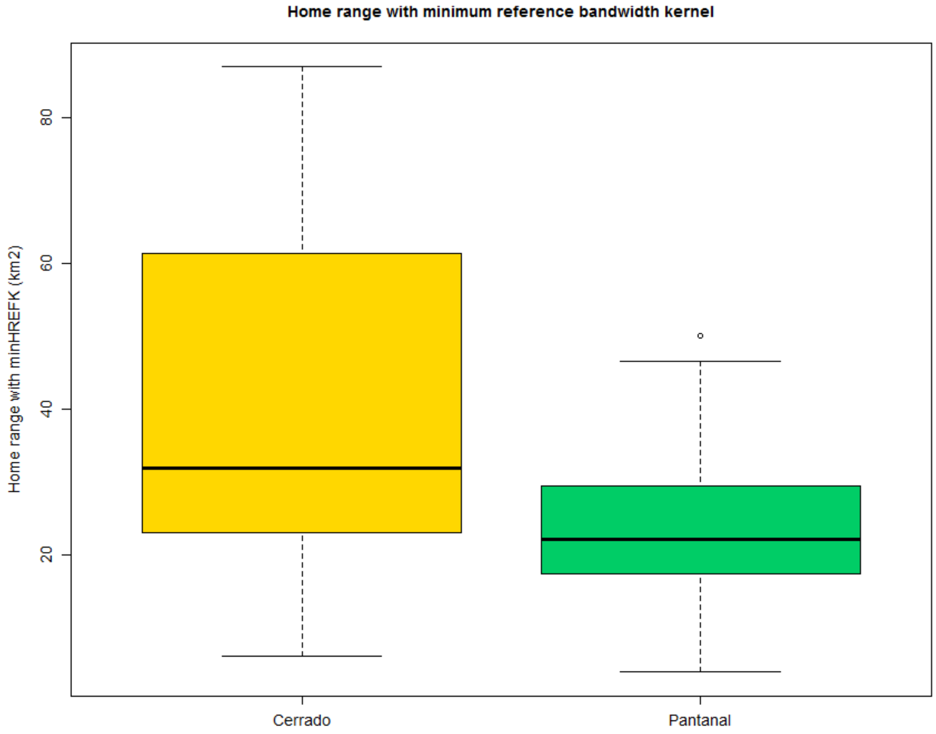
Models	AICc	dAICc	df	weight
random intercept(Biome) + Time Tracked	4.5	0.0	4	0.9936
random intercept(Biome) + Time Tracked + Slope	15	10.6	5	0.0051
random intercept(Biome) + Time Tracked + Tree cover	18.3	13.9	5	<0.001
random intercept(Biome) + Time Tracked + Edge distance	20.5	16.0	5	<0.001
random intercept(Biome) + Time Tracked + Population distance	27	22.5	5	<0.001
random intercept(Biome) + Time Tracked + Slope + Tree cover	28.8	24.4	6	<0.001
random intercept(Biome) + Time Tracked + Patch size	31.5	27.1	5	<0.001
random intercept(Biome) + Time Tracked + Road distance	32.8	28.4	5	<0.001
random intercept(Biome) + Time Tracked + Slope + Patch size	42.9	38.5	6	<0.001
random intercept(Biome) + Time Tracked + Slope + Edge distance + Patch size	59.7	55.2	7	<0.001
random intercept(Biome) + Time Tracked + Slope + Edge distance + Patch size + Treecover	71.7	67.3	8	<0.001

Table SM3. Monthly home range and mean net square displacement models for adult white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil.

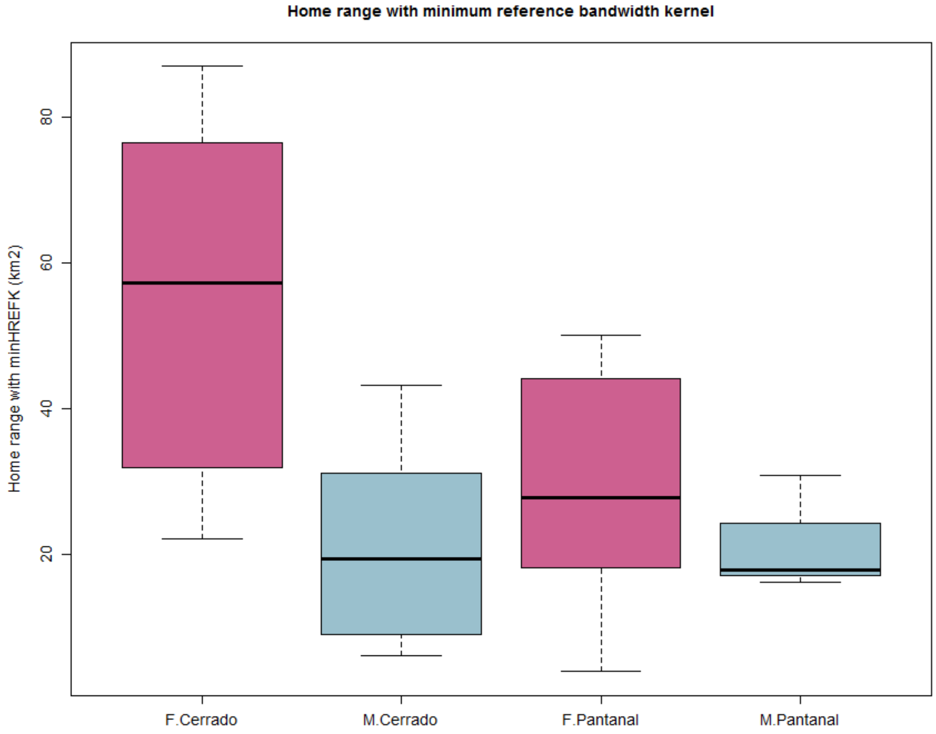
Individual	**Biome**	**Area**	**Sex**	**best MSD model**	**Monthly minHREFK 95%**	**Original total succeed fixes**	**MSDcat**
Bruna_1	Pantanal	Caiman 2	F	nullMod	12.04	2797	Null
Bruna_10	Pantanal	Caiman 2	F	NomadD	14.11	2797	Nomadic
Bruna_11	Pantanal	Caiman 2	F	HRmodA	13.43	2797	Home range
Bruna_2	Pantanal	Caiman 2	F	NomadA	24.49	2797	Nomadic
Bruna_3	Pantanal	Caiman 2	F	NomadC	27.46	2797	Nomadic
Bruna_4	Pantanal	Caiman 2	F	NomadC	25.62	2797	Nomadic
Bruna_5	Pantanal	Caiman 2	F	NomadD	17.95	2797	Nomadic
Bruna_6	Pantanal	Caiman 2	F	Dispmod2	44.01	2797	Dispersal
Bruna_7	Pantanal	Caiman 2	F	NomadC	23.98	2797	Nomadic
Bruna_8	Pantanal	Caiman 2	F	NomadD	21.89	2797	Nomadic
Bruna_9	Pantanal	Caiman 2	F	Dispmod2	16.85	2797	Dispersal
Canela_1	Pantanal	Barranco Alto	F	NomadC	25.48	1165	Nomadic
Canela_2	Pantanal	Barranco Alto	F	Dispmod1	12.46	1165	Dispersal
Canela_3	Pantanal	Barranco Alto	F	NomadC	11.20	1165	Nomadic
Canela_4	Pantanal	Barranco Alto	F	NomadC	14.98	1165	Nomadic
Cida_1	Cerrado	Safira	F	NomadD	140.95	1293	Nomadic
Cida_2	Cerrado	Safira	F	NomadA	39.95	1293	Nomadic
Cida_3	Cerrado	Safira	F	Dispmod2	41.71	1293	Dispersal
Cida_4	Cerrado	Safira	F	NomadC	62.73	1293	Nomadic
Cida_5	Cerrado	Safira	F	Dispmod2	39.30	1293	Dispersal
Claudio_1	Pantanal	23 de Marco	M	Dispmod1	20.74	275	Dispersal
Claudio_2	Pantanal	23 de Marco	M	NomadA	26.53	275	Nomadic
Cleide_1	Cerrado	Jacobina	F	NomadD	31.70	1760	Nomadic
Cleide_2	Cerrado	Jacobina	F	Dispmod2	25.65	1760	Dispersal
Cleide_3	Cerrado	Jacobina	F	Dispmod3	11.87	1760	Dispersal
Cleide_4	Cerrado	Jacobina	F	Dispmod2	16.81	1760	Dispersal
Cleide_5	Cerrado	Jacobina	F	Dispmod2	48.97	1760	Dispersal
Cleide_6	Cerrado	Jacobina	F	NomadC	24.05	1760	Nomadic
Cleide_7	Cerrado	Jacobina	F	Dispmod1	17.77	1760	Dispersal
Jay_1	Cerrado	Colorado	M	NomadD	22.30	380	Nomadic
Jay_2	Cerrado	Colorado	M	NomadD	25.13	380	Nomadic
Jay_3	Cerrado	Colorado	M	NomadA	19.91	380	Nomadic
Julia_1	Cerrado	Claudia	F	NomadA	60.77	349	Nomadic
Julia_2	Cerrado	Claudia	F	Dispmod2	54.03	349	Dispersal
Julia_3	Cerrado	Claudia	F	NomadC	8.70	349	Nomadic
Lucas_1	Pantanal	Barranco Alto	M	Dispmod3	21.01	457	Dispersal

Lurdes_1	Cerrado	Colorado	F	NomadA	9.39	462	Nomadic
Lurdes_2	Cerrado	Colorado	F	NomadA	3.95	462	Nomadic
Lurdes_3	Cerrado	Colorado	F	Dispmod2	4.63	462	Dispersal
Lurdes_4	Cerrado	Colorado	F	Dispmod2	17.55	462	Dispersal
Lurdes_5	Cerrado	Colorado	F	NomadD	7.12	462	Nomadic
Malu_1	Cerrado	Safira	F	Dispmod3	35.14	504	Dispersal
Malu_2	Cerrado	Safira	F	Dispmod3	11.90	504	Dispersal
Malu_3	Cerrado	Safira	F	NomadD	35.01	504	Nomadic
Malu_4	Cerrado	Safira	F	Dispmod3	11.25	504	Dispersal
Malu_5	Cerrado	Safira	F	NomadC	5.33	504	Nomadic
MaluII_1	Cerrado	Safira	F	NomadC	12.07	733	Nomadic
MaluII_2	Cerrado	Safira	F	NomadD	47.94	733	Nomadic
MaluII_3	Cerrado	Safira	F	Dispmod2	61.40	733	Dispersal
Marcello_1	Pantanal	Caiman 1	M	NomadD	12.13	1246	Nomadic
Marcello_2	Pantanal	Caiman 1	M	Dispmod1	16.89	1246	Dispersal
Marcello_3	Pantanal	Caiman 1	M	NomadA	10.60	1246	Nomadic
Marcello_4	Pantanal	Caiman 1	M	NomadA	5.82	1246	Nomadic
Marcello_5	Pantanal	Caiman 1	M	NomadA	12.04	1246	Nomadic
Mario_1	Pantanal	Caiman 2	M	nullMod	14.77	990	Null
Mario_2	Pantanal	Caiman 2	M	NomadA	28.70	990	Nomadic
Mario_3	Pantanal	Caiman 2	M	NomadD	25.23	990	Nomadic
Mario_4	Pantanal	Caiman 2	M	NomadC	29.06	990	Nomadic
Nanda_1	Pantanal	Barranco Alto	F	nullMod	20.80	1584	Null
Nanda_2	Pantanal	Barranco Alto	F	NomadA	9.40	1584	Nomadic
Nanda_3	Pantanal	Barranco Alto	F	NomadC	11.39	1584	Nomadic
Nanda_4	Pantanal	Barranco Alto	F	Dispmod1	10.60	1584	Dispersal
Nanda_5	Pantanal	Barranco Alto	F	NomadA	7.64	1584	Nomadic
Nanda_6	Pantanal	Barranco Alto	F	HRmodA	21.45	1584	Home range
Norma_1	Pantanal	23 de Marco	F	Dispmod1	24.80	507	Dispersal
Norma_2	Pantanal	23 de Marco	F	NomadD	49.99	507	Nomadic
Norma_3	Pantanal	23 de Marco	F	NomadD	20.57	507	Nomadic
Norma_4	Pantanal	23 de Marco	F	nullMod	48.97	507	Null
Pumba_1	Pantanal	23 de Marco	F	Dispmod3	20.08	1800	Dispersal
Pumba_2	Pantanal	23 de Marco	F	NomadD	41.69	1800	Nomadic
Pumba_3	Pantanal	23 de Marco	F	NomadC	48.62	1800	Nomadic
Pumba_4	Pantanal	23 de Marco	F	Dispmod2	41.52	1800	Dispersal
Pumba_5	Pantanal	23 de Marco	F	NomadC	17.95	1800	Nomadic
Pumba_6	Pantanal	23 de Marco	F	Dispmod2	46.98	1800	Dispersal
Pumba_7	Pantanal	23 de Marco	F	NomadD	41.97	1800	Nomadic
Roberta_1	Pantanal	Caiman 1	F	NomadD	36.28	2935	Nomadic
Roberta_10	Pantanal	Caiman 1	F	Dispmod1	44.48	2935	Dispersal
Roberta_11	Pantanal	Caiman 1	F	NomadD	10.62	2935	Nomadic
Roberta_12	Pantanal	Caiman 1	F	NomadD	20.06	2935	Nomadic
Roberta_2	Pantanal	Caiman 1	F	NomadD	8.68	2935	Nomadic

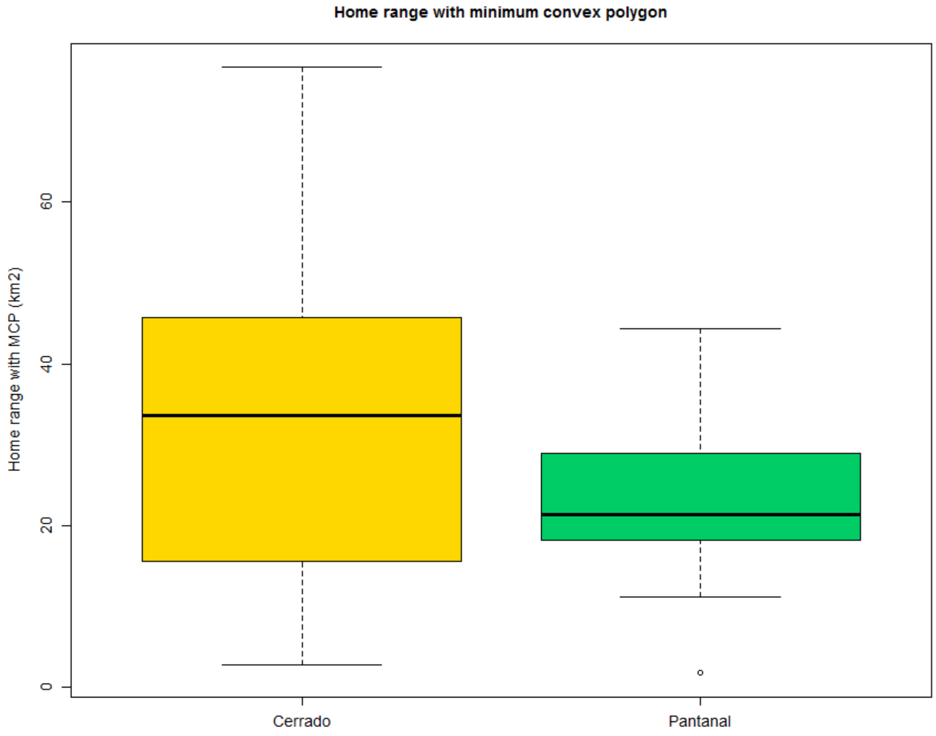
Roberta_3	Pantanal	Caiman 1	F	HRmodB	15.86	2935	Home range
Roberta_4	Pantanal	Caiman 1	F	NomadA	15.62	2935	Nomadic
Roberta_5	Pantanal	Caiman 1	F	NomadC	17.64	2935	Nomadic
Roberta_6	Pantanal	Caiman 1	F	NomadA	17.74	2935	Nomadic
Roberta_7	Pantanal	Caiman 1	F	nullMod	19.49	2935	Null
Roberta_8	Pantanal	Caiman 1	F	NomadA	15.63	2935	Nomadic
Roberta_9	Pantanal	Caiman 1	F	NomadD	28.87	2935	Nomadic
Rosana_1	Pantanal	23 de Marco	F	NomadC	12.37	1240	Nomadic
Rosana_2	Pantanal	23 de Marco	F	NomadD	20.71	1240	Nomadic
Rosana_3	Pantanal	23 de Marco	F	NomadA	22.53	1240	Nomadic
Rosana_4	Pantanal	23 de Marco	F	NomadA	16.01	1240	Nomadic
Rosana_5	Pantanal	23 de Marco	F	Dispmod1	28.05	1240	Dispersal
Tereza_1	Cerrado	Santa Tereza	F	Dispmod3	93.94	110	Dispersal
Toninho_1	Cerrado	Safira	M	Dispmod3	35.03	397	Dispersal
Toninho_2	Cerrado	Safira	M	HRmodA	33.99	397	Home range
Toninho_3	Cerrado	Safira	M	Dispmod3	22.47	397	Dispersal
Trina_1	Pantanal	Barranco Alto	F	NomadD	20.66	1598	Nomadic
Trina_2	Pantanal	Barranco Alto	F	HRmodA	20.10	1598	Home range
Trina_3	Pantanal	Barranco Alto	F	NomadA	13.02	1598	Nomadic
Trina_4	Pantanal	Barranco Alto	F	NomadA	15.53	1598	Nomadic
Trina_5	Pantanal	Barranco Alto	F	NomadA	16.09	1598	Nomadic
Trina_6	Pantanal	Barranco Alto	F	NomadD	16.67	1598	Nomadic
Vagner_1	Cerrado	Taboco	M	Dispmod2	53.26	1151	Dispersal
Vagner_2	Cerrado	Taboco	M	Dispmod2	8.64	1151	Dispersal
Vagner_3	Cerrado	Taboco	M	NomadD	37.12	1151	Nomadic
Vagner_4	Cerrado	Taboco	M	NomadC	7.23	1151	Nomadic
Valentina_1	Cerrado	Santa Tereza	F	Dispmod1	14.64	1167	Dispersal
Valentina_2	Cerrado	Santa Tereza	F	Dispmod1	24.79	1167	Dispersal
Valentina_3	Cerrado	Santa Tereza	F	Dispmod3	143.60	1167	Dispersal
Valentina_4	Cerrado	Santa Tereza	F	Dispmod3	33.09	1167	Dispersal



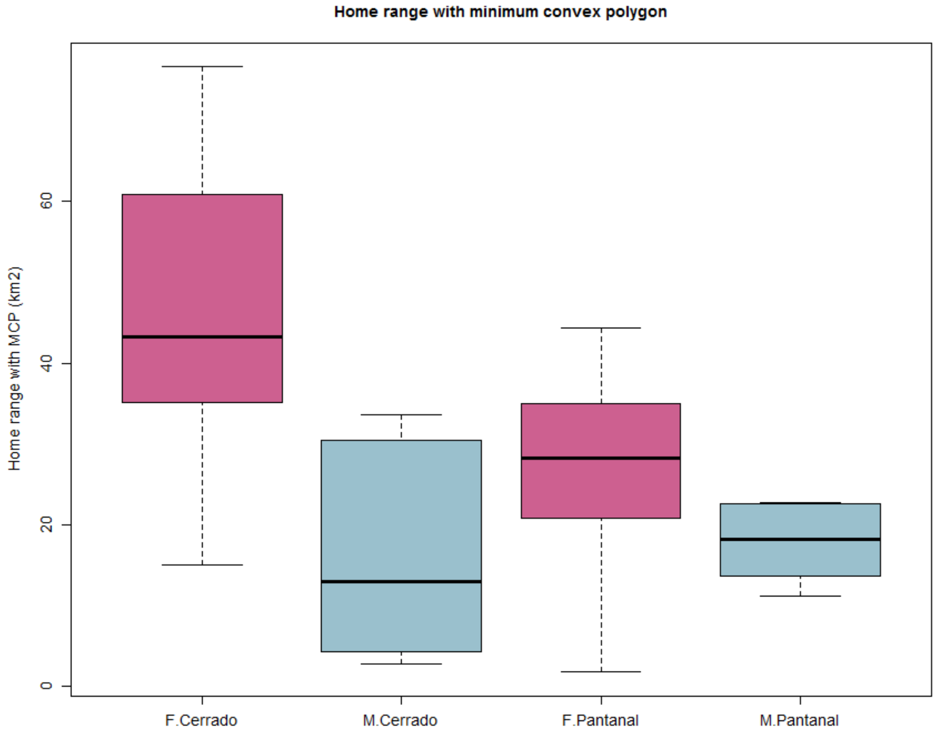
SM4. Home range size (in km^2) of white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with fixed kernel and minimum reference bandwidth (minHREFK).



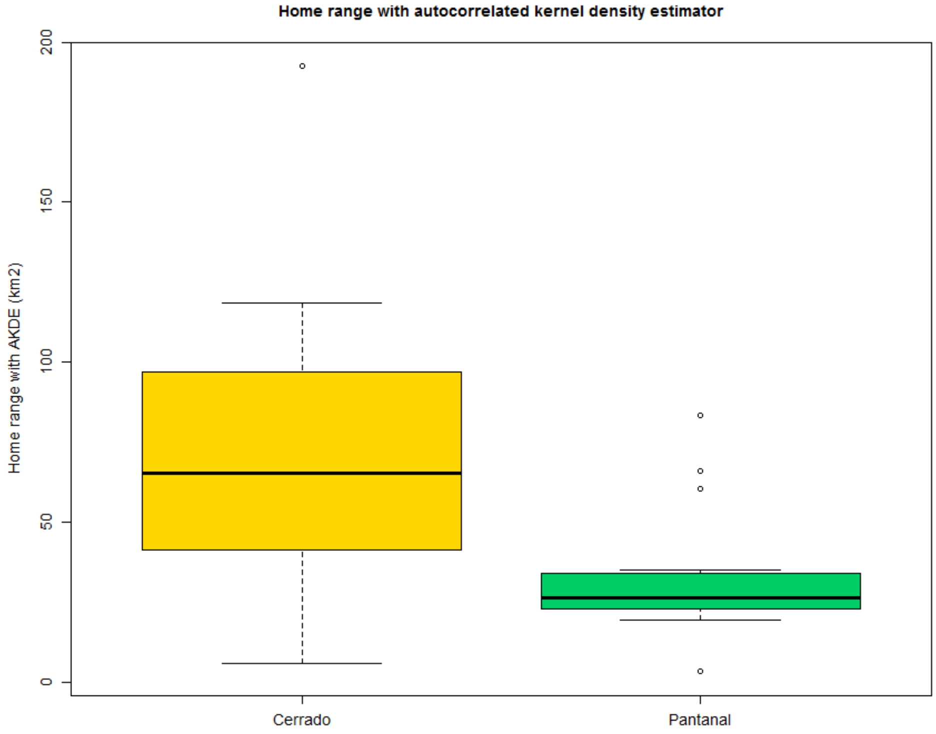
SM5. Home range size (in km^2) of males (M) and females (F) white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with fixed kernel and minimum reference bandwidth (minHREFK).



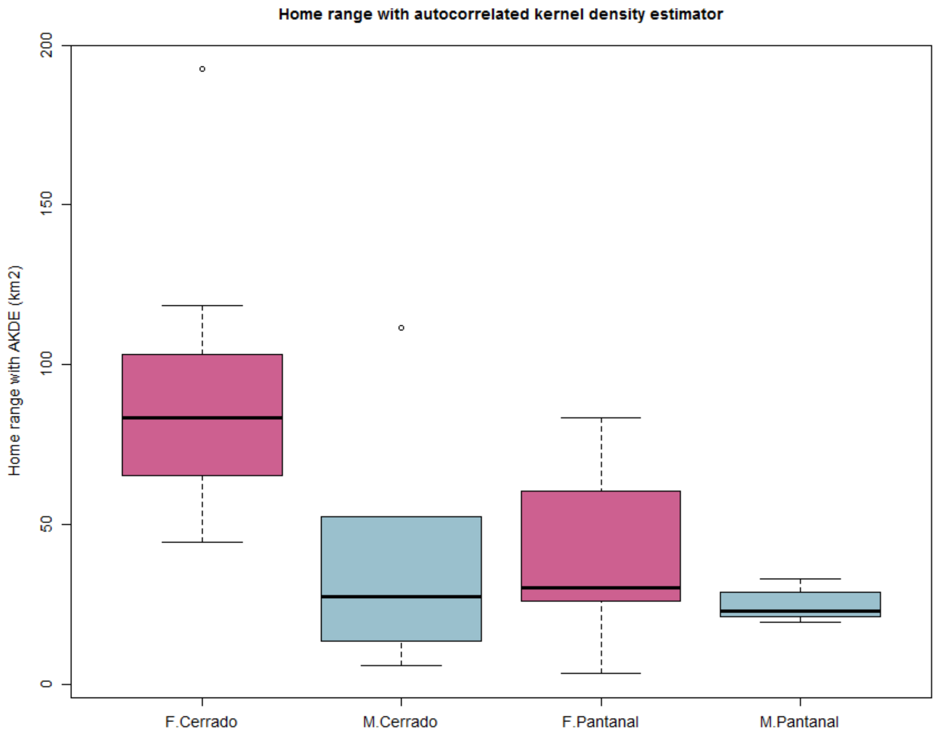
SM6. Home range size (in km^2) of white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with the minimum convex polygon (MCP).



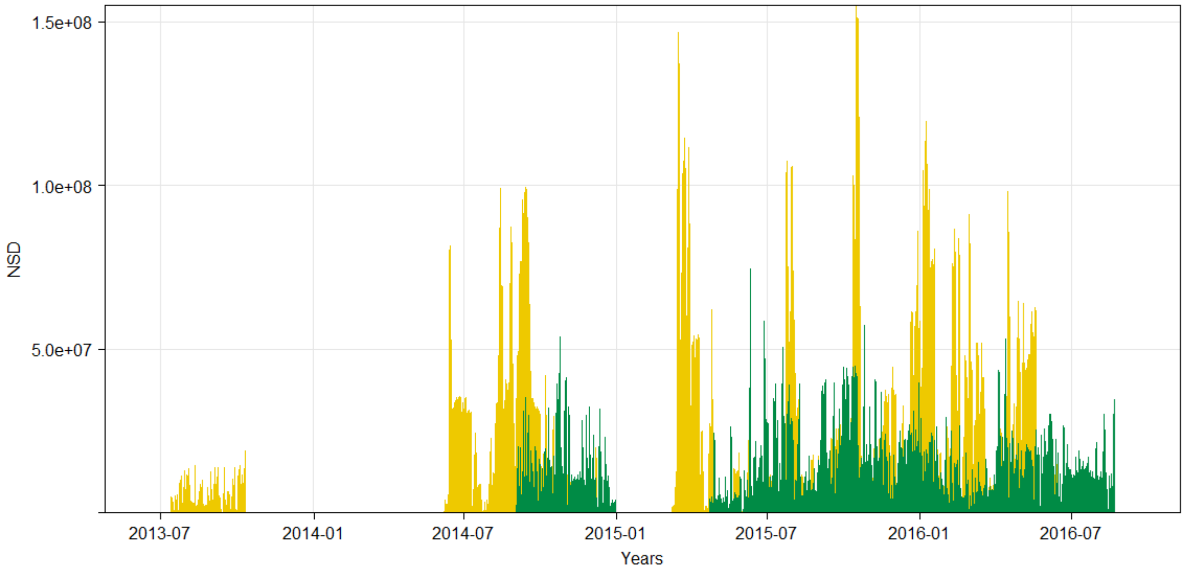
SM7. Home range size (in km^2) of males (M) and females (F) white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with the minimum convex polygon (MCP).



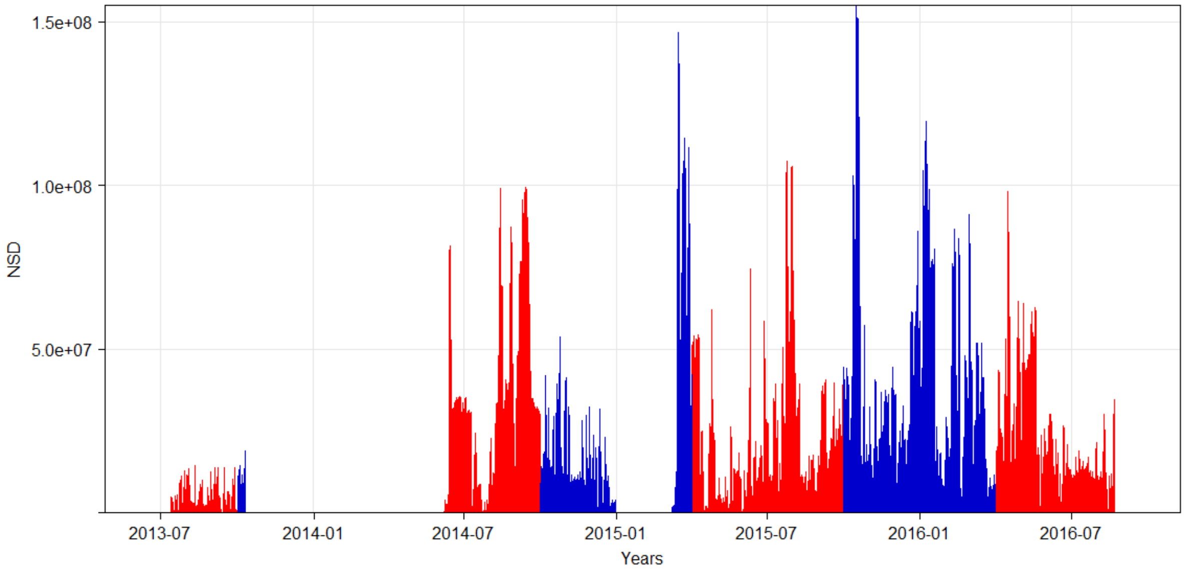
SM8. Home range size (in km^2) of white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with the autocorrelated kernel density estimator (AKDE).



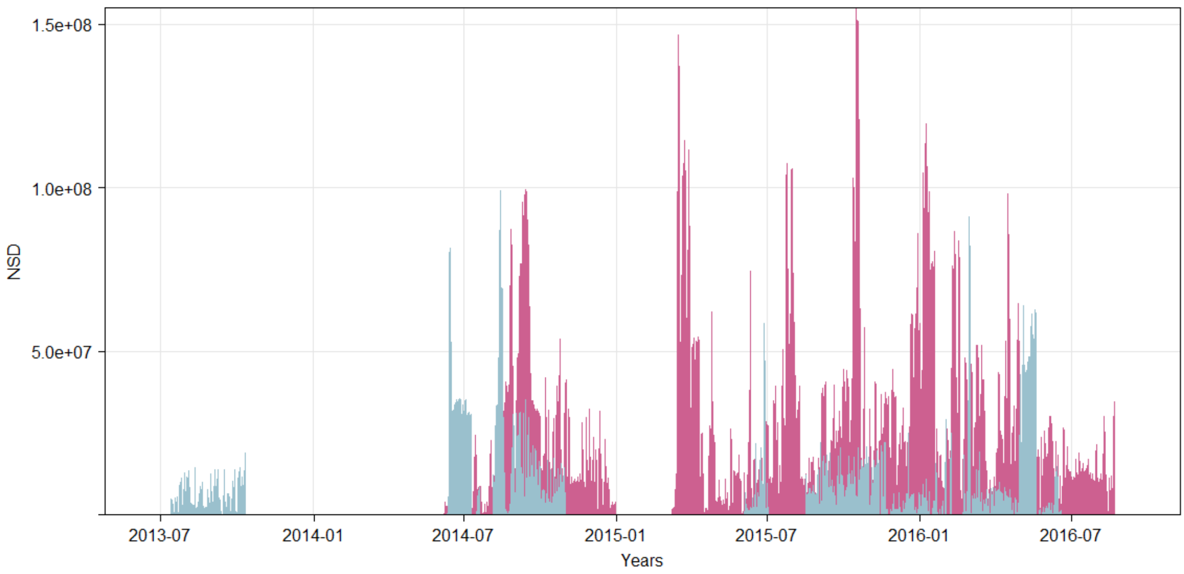
SM9. Home range size (in km^2) of males (M) and females (F) white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars in Cerrado and in Pantanal of Mato Grosso do Sul state, Brazil. Home range size was estimated with the autocorrelated kernel density estimator (AKDE).



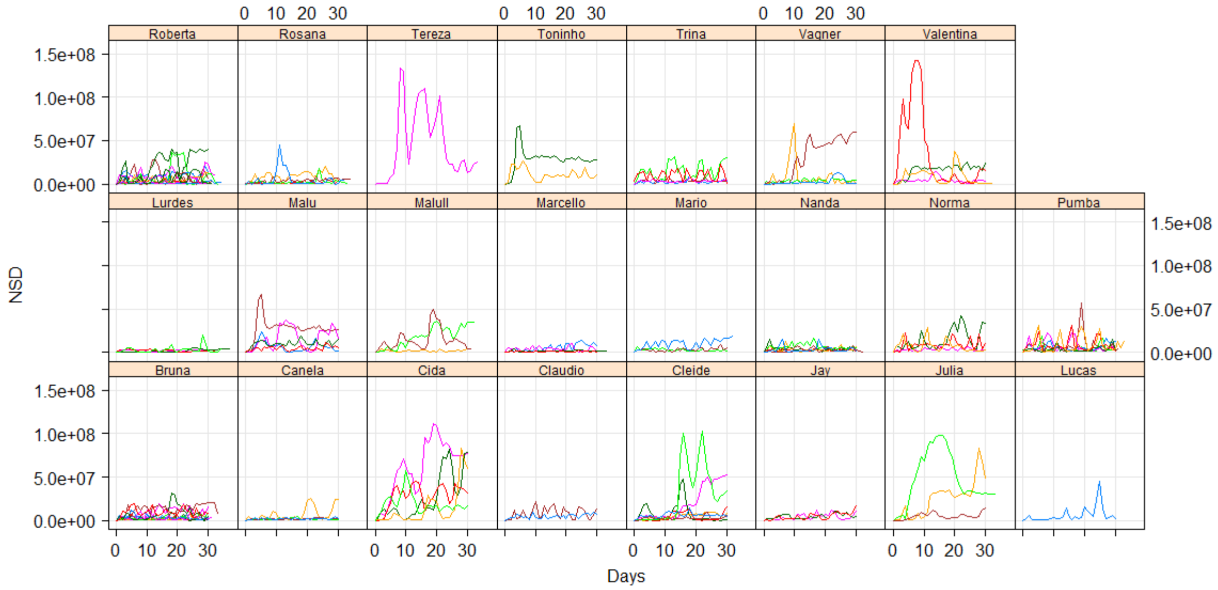
SM10. Net square displacement of white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars from 2013 to 2016 in the Cerrado (yellow) and in Pantanal (green) of Mato Grosso do Sul state, Brazil.



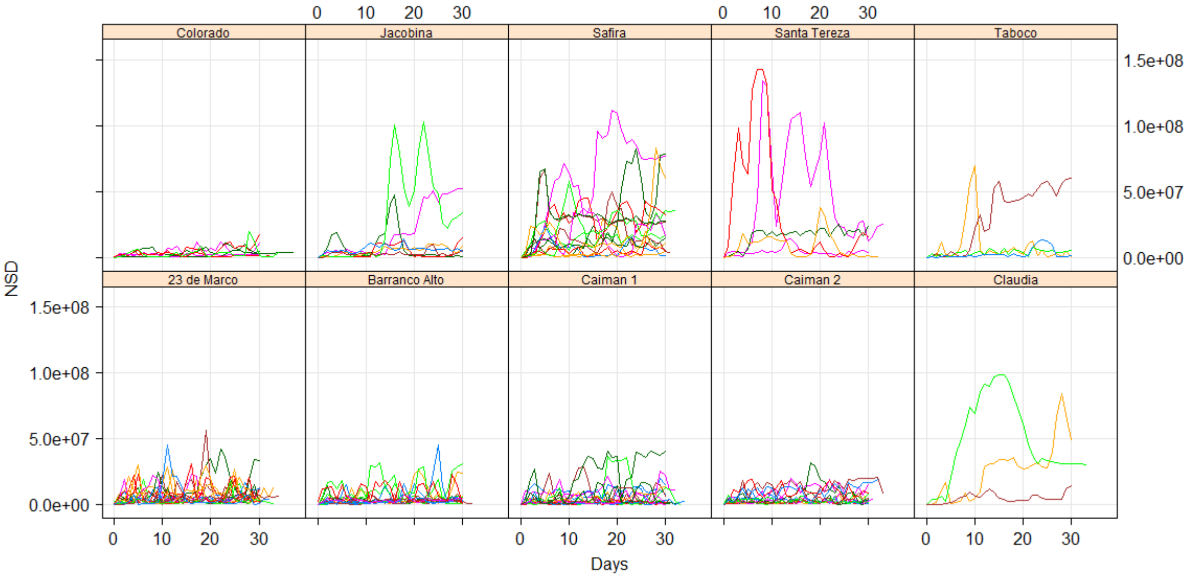
SM11. Net square displacement of white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars from 2013 to 2016 in the dry (red) and wet (blue) seasons of Mato Grosso do Sul state, Brazil.



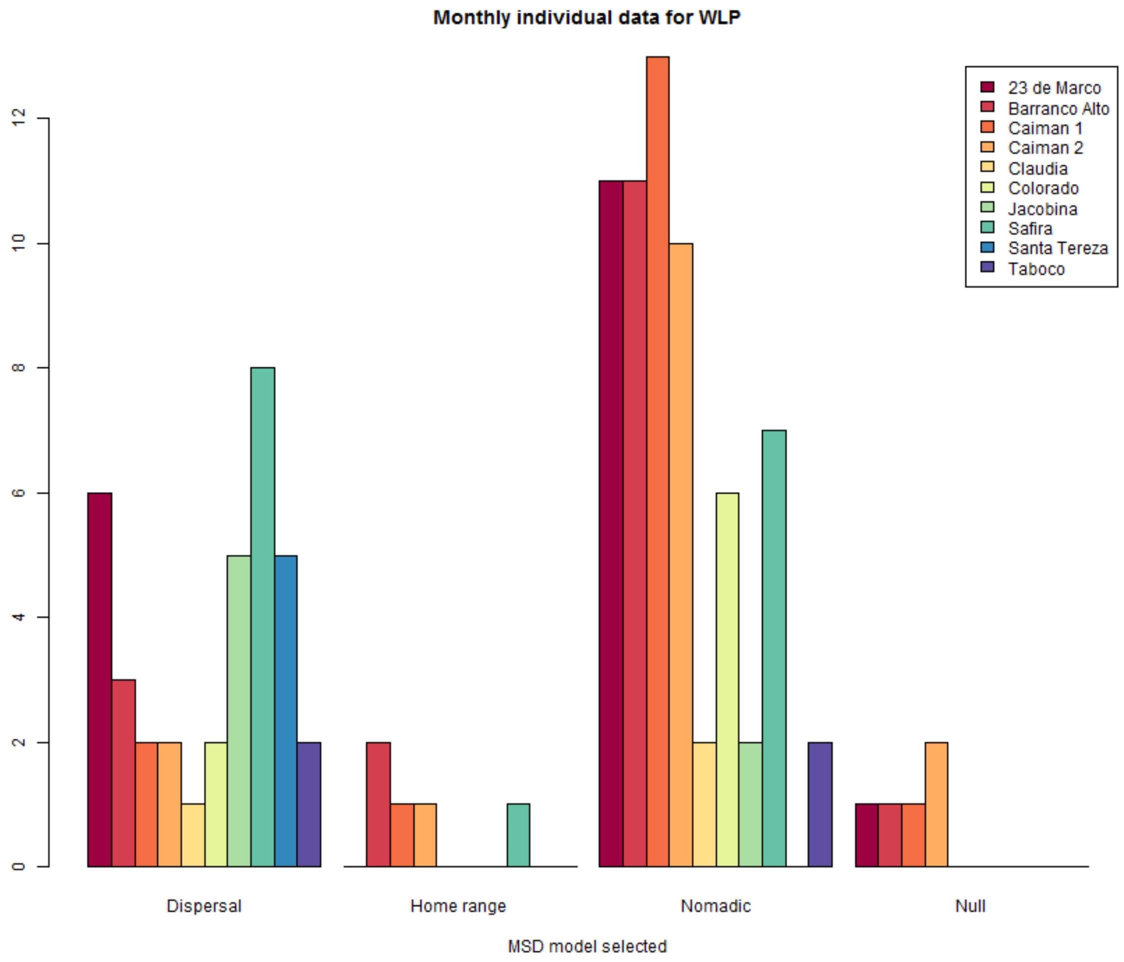
SM12. Net square displacement of males (light blue) and females (pink) white-lipped peccaries (*Tayassu pecari*) monitored with GPS collars from 2013 to 2016 in Mato Grosso do Sul state, Brazil.



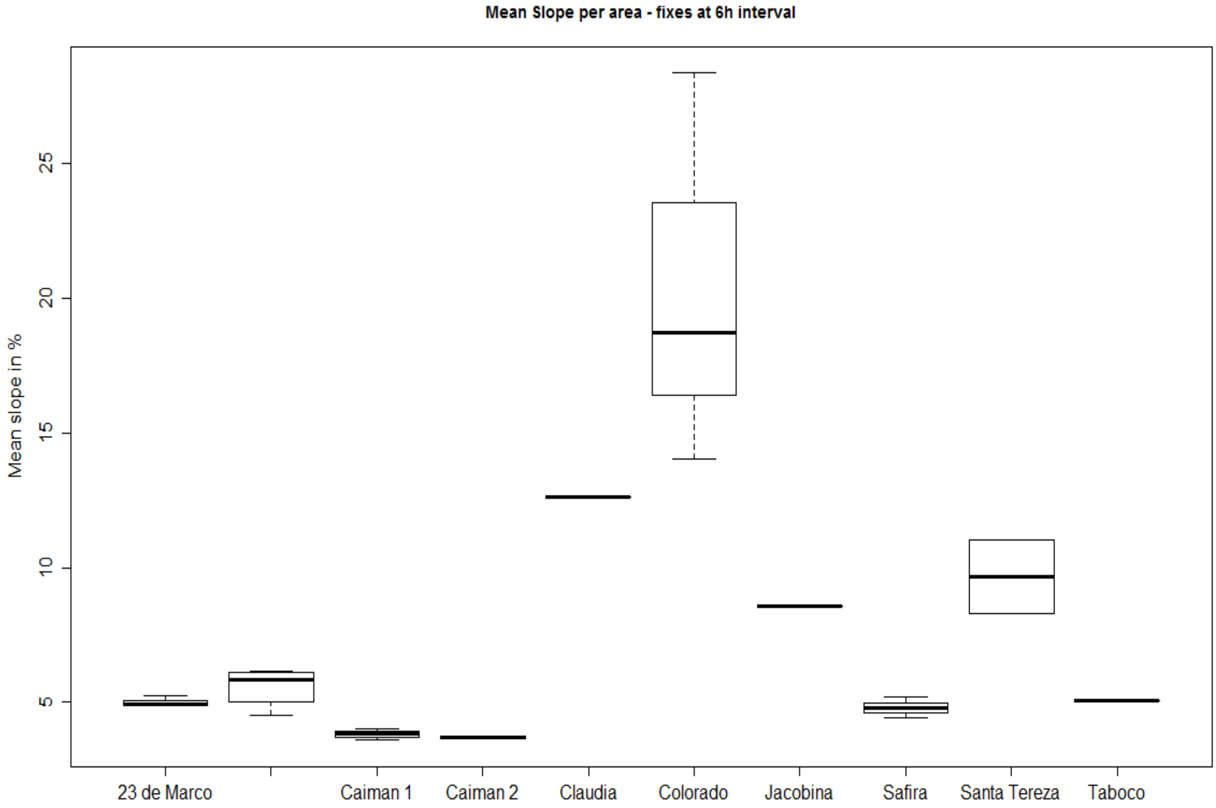
SM13. Monthly net square displacement analysis for white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



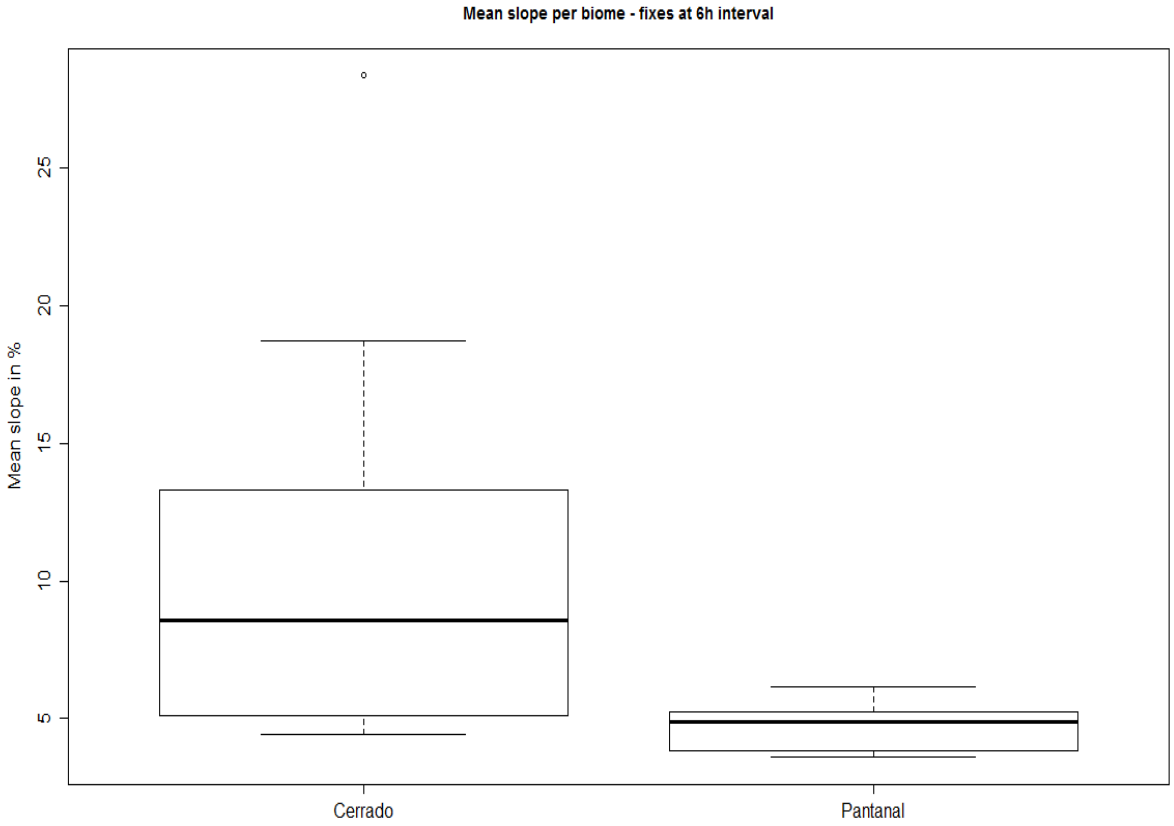
SM14. Monthly net square displacement analysis for white-lipped peccary (*Tayassu pecari*) herds monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



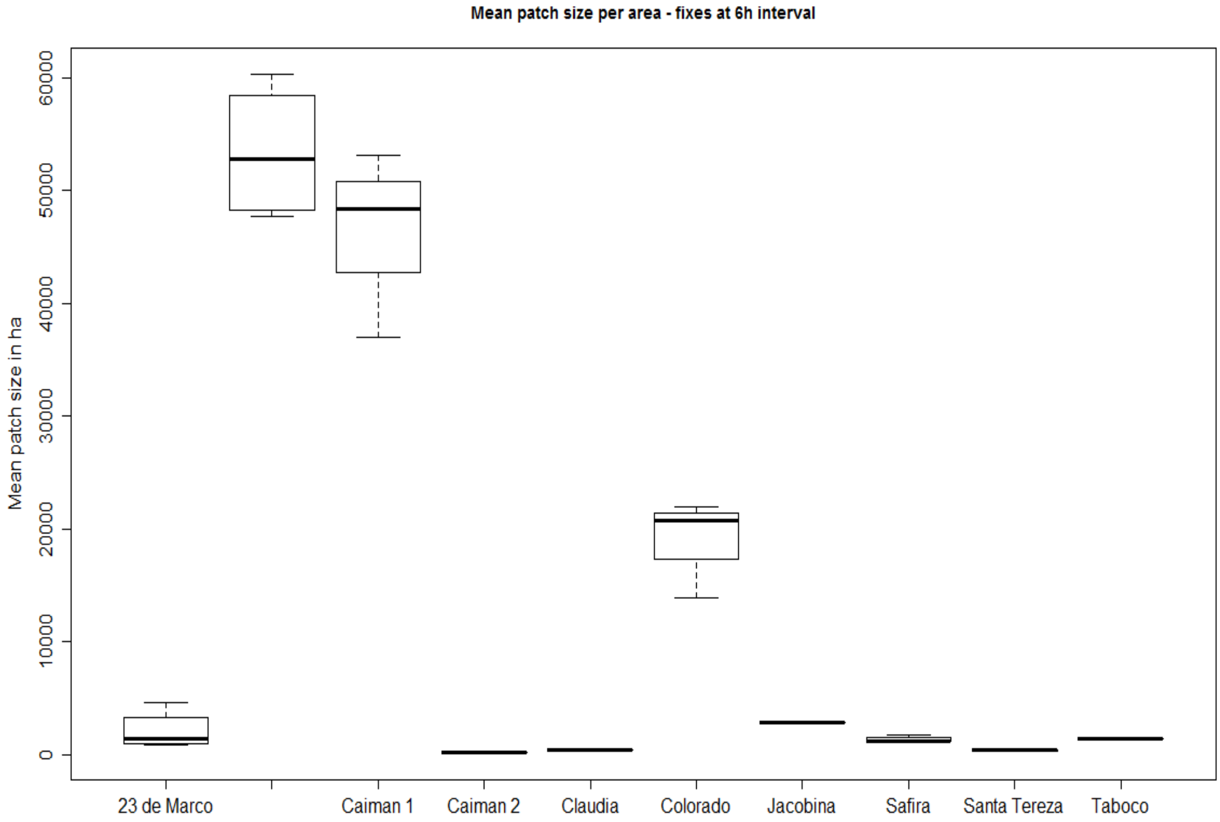
SM15. Monthly mean net square displacement results showing the number of the white-lipped peccaries (*Tayassu pecari*) monthly data classified in each movement behaviour category. Herds were monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



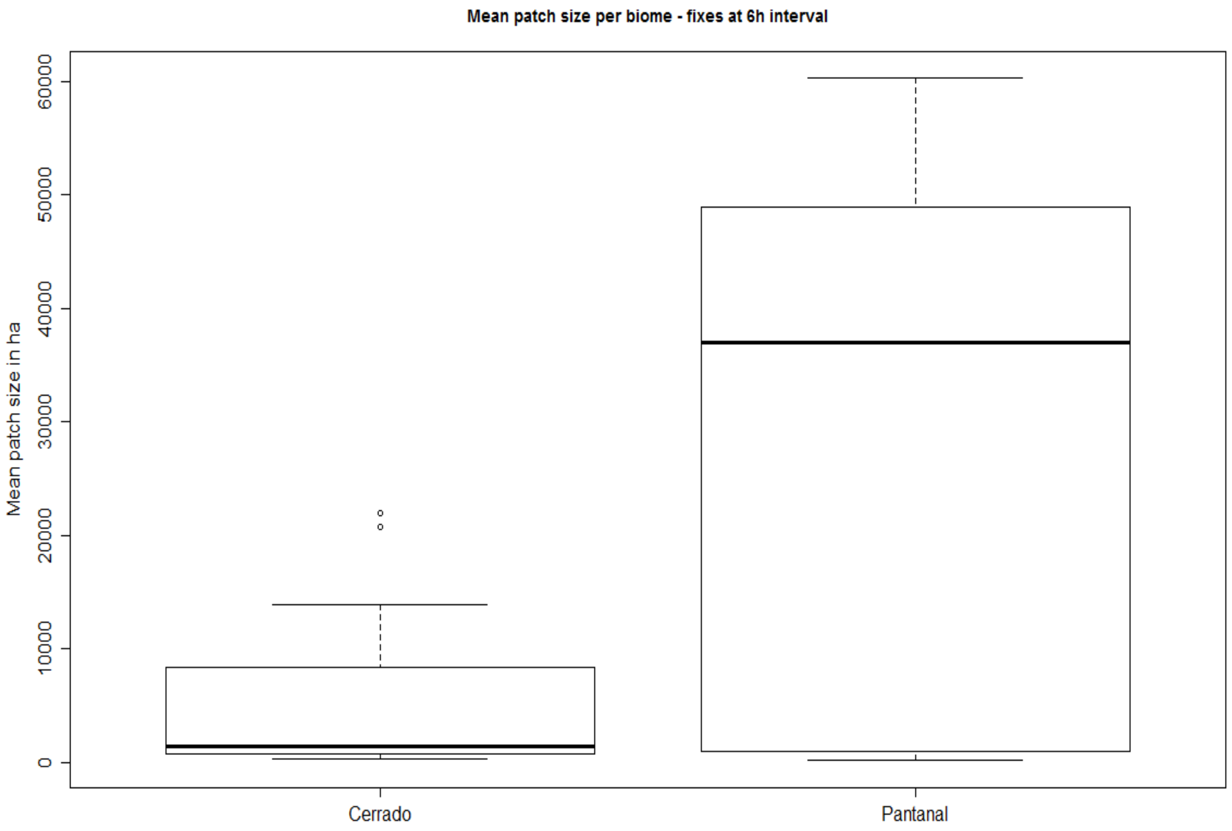
SM16. Mean slope values (in %) associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



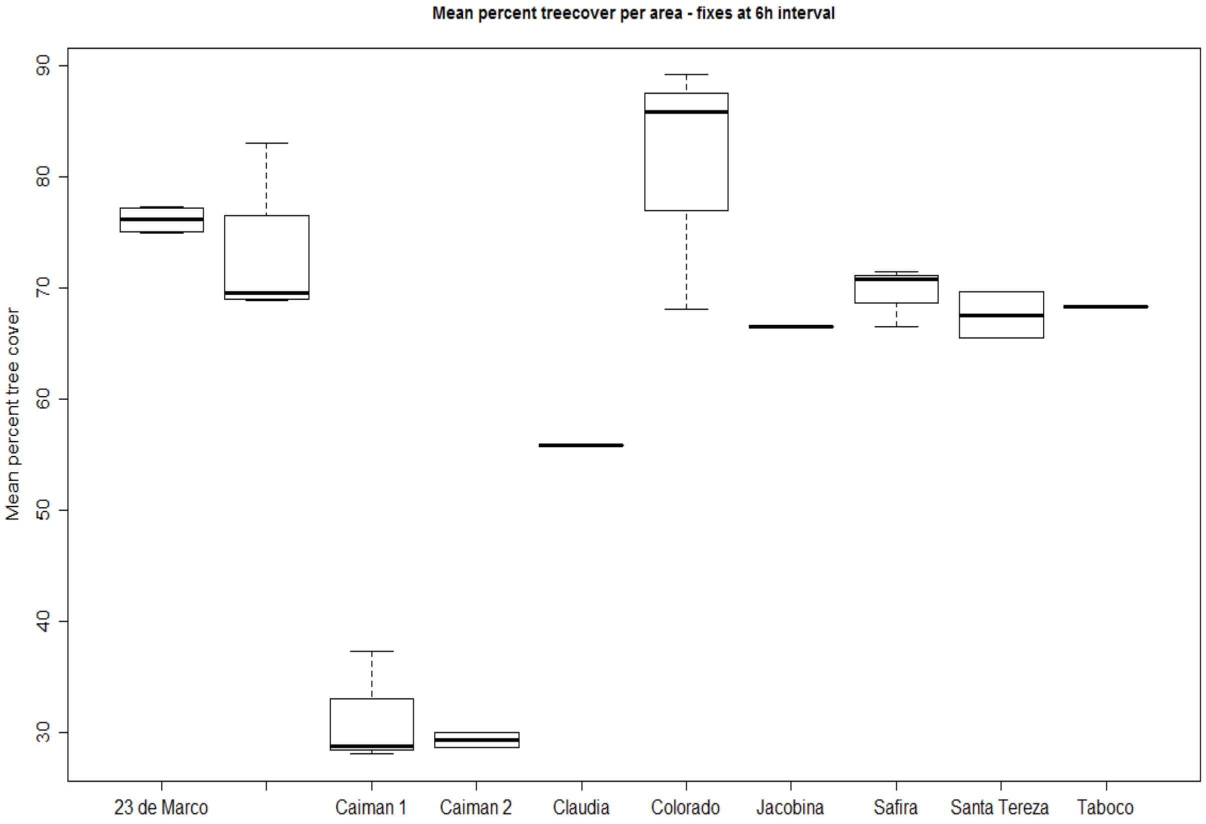
SM17. Mean slope values (in %) associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



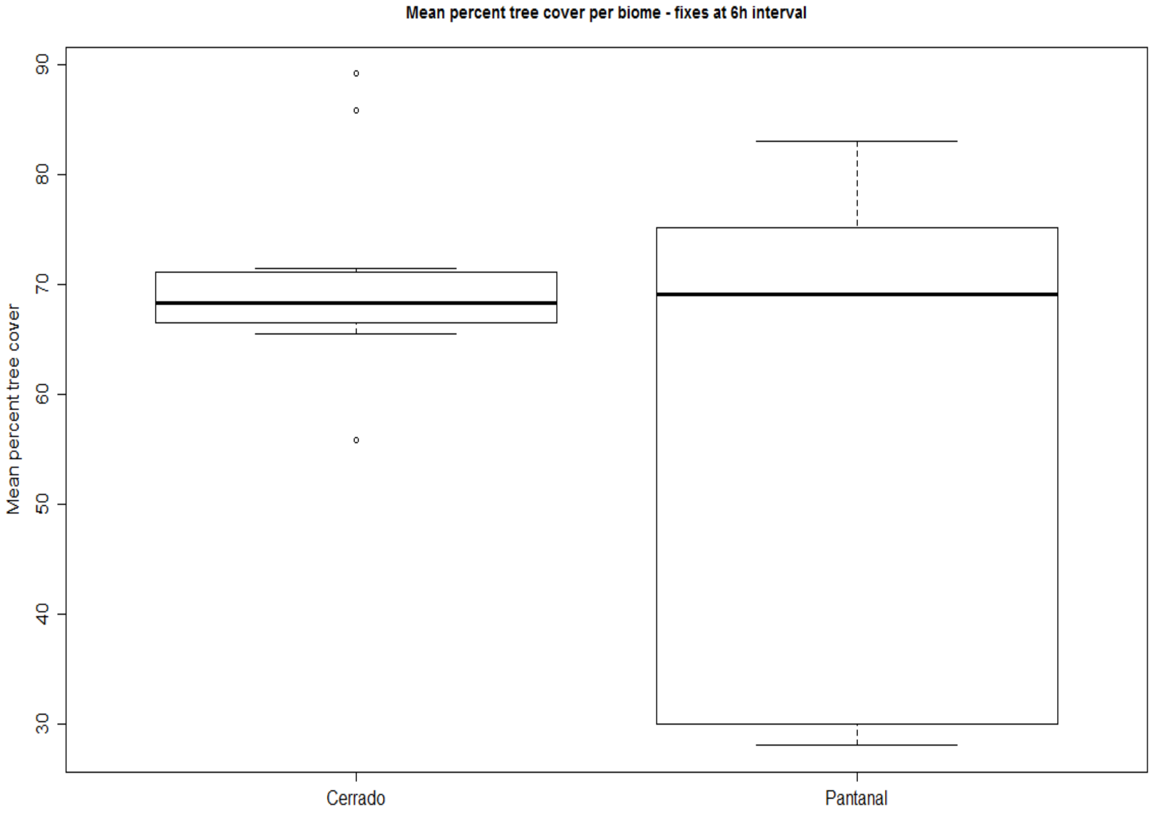
SM18. Mean patch size (in ha) values associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



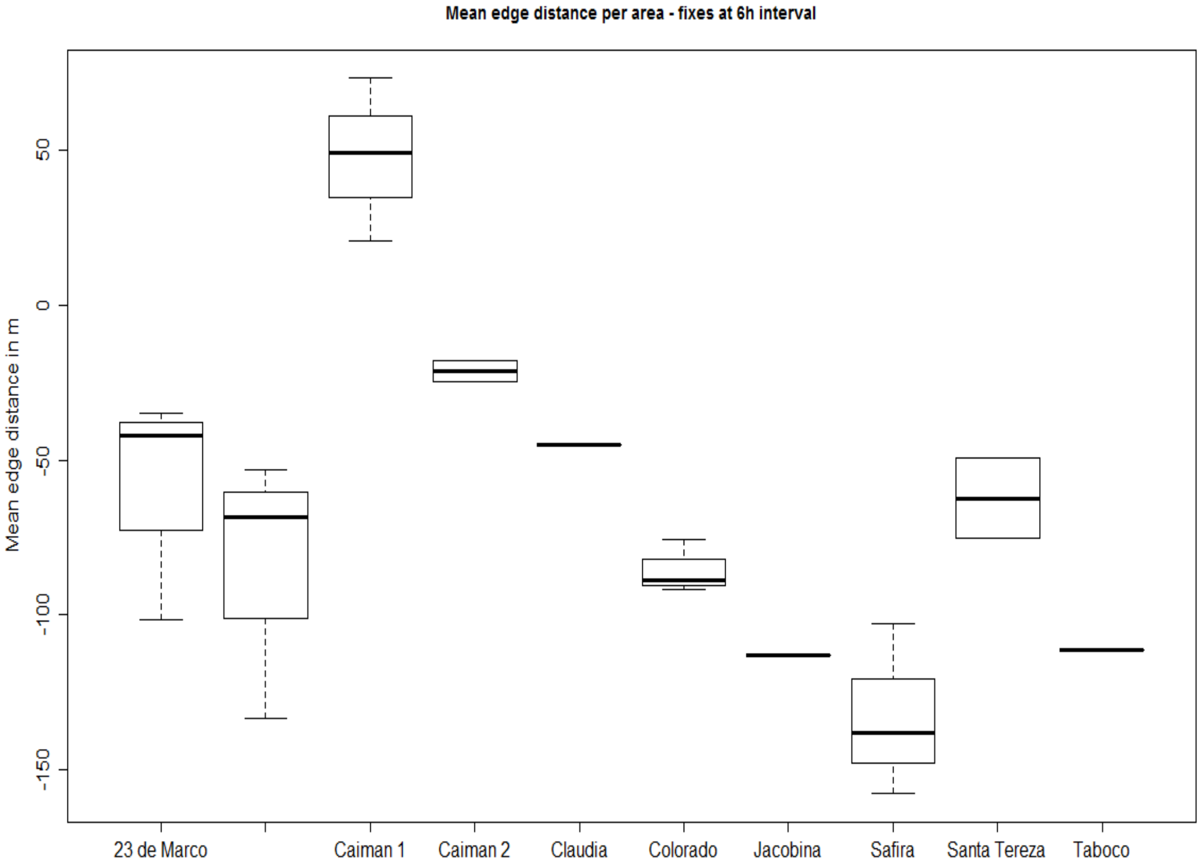
SM19. Mean patch size (in ha) values associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



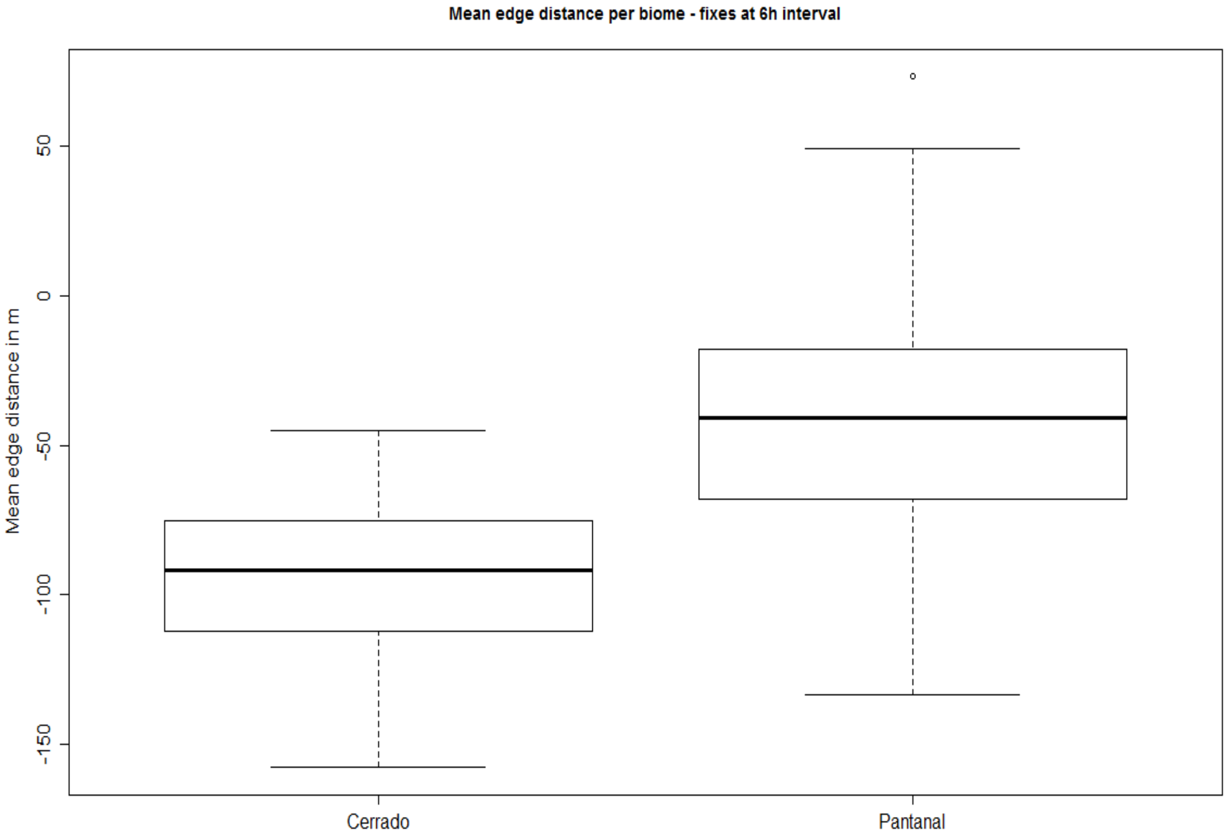
SM20. Mean percent tree cover values associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



SM21. Mean percent tree cover values associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



SM21. Mean edge distance values (in meters) associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.



SM22. Mean edge distance values (in meters) associated with GPS positions of the white-lipped peccaries (*Tayassu pecari*) monitored in the Cerrado and Pantanal of Mato Grosso do Sul state, Brazil, between 2013 and 2016.