





Permeability of Neotropical agricultural lands to a key native ungulate—Are well-connected forests important?

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Funding information

FAPESP, Grant/Award Number: 2013/50421-2 and 2014/23132-2; CNPq, Grant/Award Number: 312045/2013-1, 312292/2016-3 and 161089/2014-3; Silicon Valley Community Foundation; The Overbrook Foundation; International ReSource Award; WCS Brasil; Vanderbilt University; PROCAD/CAPES, Grant/Award Number: 88881.068425/2014-01

Associate Editor: Jennifer Powers

Handling Editor: Jayashree Ratnam

Abstract

Much of what remains of the Earth's tropical forests is embedded within agricultural landscapes, where forest is reduced and fragmented. As native forest ungulates are critical to maintaining forest function, it is imperative to understand how this functional group responds to declines in forest cover and connectivity resulting from agricultural expansion. We addressed this issue by evaluating selection of forest cover and forest connectivity by a key native ungulate of Neotropical forests, the white-lipped peccary (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla), in agricultural landscapes of Brazil. We evaluated selection using compositional analysis at two hierarchical levels, landscape, and home range. From 2013 to 2019, we GPS-tracked eight white-lipped peccary herds in Southwest Brazil, resulting in a total of 14,460 GPS locations. We found that herds can live in landscapes with a wide range of forest cover (35%–81% of home ranges covered by native forest), with significant, but not strong, selection at the landscape level ($p = .045$). Nevertheless, herds strongly select for forest cover within their home ranges (81%–97% of locations within native forest; highly significant selection at the home-range level: $p = .008$). As for connectivity, herds significantly select the largest, most connected forest fragments at the landscape level ($p = .04$), but not at the home-range level ($p = .07$). Our results support that Neotropical forests within agricultural landscapes need to be well connected in order to preserve this key native ungulate and maintain long-term forest function.

Abstract in Portuguese is available with online material.

KEYWORDS

Brazilian Cerrado, functional connectivity, landscape ecology, movement ecology, white-lipped peccaries

1 | INTRODUCTION

Tropical forests are essential for maintaining high levels of biodiversity and ecosystem services worldwide (Thompson et al., 2011), and much of what remains is embedded in agricultural lands (Ellis & Ramankutty, 2008; Mendenhall, Shields-Estrada, Krishnaswami, &

Daily, 2016). Such a scenario places high priority on preserving tropical forests in agricultural landscapes (Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013). To ensure that tropical forests in agricultural landscapes are sustainable in the long run, key players of forest dynamics must also persist within the forest remains. Among those key players are forest ungulates. They promote long-distance

seed dispersal (Corlett, 2017; Jara-Guerrero, Escribano-Avila, Espinosa, De la Cruz, & Méndez, 2018; Paolucci et al., 2019), soil disturbance (Keuroghlian & Eaton, 2009; Pastor et al., 1998), nutrient deposition (Berzaghi et al., 2018), and seed and seedling predation (Bodmer, 2001; Keuroghlian & Eaton, 2008). In addition, forest ungulates act as long-distance links of forest processes such that their disappearance can have irreversible, negative effects on forest regeneration (Beck, Mauricio, Duarte, & Reyna-Hurtado, 2016; Galetti, Bovendorp, & Guevara, 2015; Sobral et al., 2017; Villar et al., 2020).

Forest ungulates are negatively impacted by human activities (Jorge, Galetti, Ribeiro, & Ferraz, 2013), especially hunting and poaching (Ripple et al., 2015), which increase in agricultural lands, due to greater accessibility to natural forest patches (Peres, Thaise, Schietti, Desmoulières, & Levi, 2015). Less understood is how forest ungulates are affected by physical changes in the amount and configuration of forests when forests are replaced by croplands or pasture. The fragmentation process implies changes in habitat features, such as connectivity and cover (Fahrig, 2003). Changes in forest connectivity should affect ecological processes associated with displacement through the landscape, whereas forest cover should affect ecological processes associated with the amount and the spatial configuration of resource availability (e.g., how much food is left and how spatially distributed it is—Fahrig, 2007). As forests are reduced and fragmented, two nested questions arise:

1. Will forest ungulates continue to rely on the remaining forests and forest resources, and therefore continue to mainly use forest patches? Or will they increasingly use the matrix as it increases in proportion in the landscape?
2. In the case that forest ungulates continue to be forest-dwellers, to what extent will they cross the matrix to reach isolated forest fragments?

In order to address those questions, we use the largest herd-forming and widest-ranging ungulate of Neotropical forests, the white-lipped peccary (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla; hereafter WLP). WLP adult body size averages 35 kg, and they can live in herds of more than 100 individuals (Beck, Keuroghlian, Reyna-Hurtado, Altrichter, & Gongora, 2017), which makes them the largest vertebrate biomass of Neotropical forests where they are still present (Kiltie & Terborgh, 1983). They also have the widest ranges reported for Neotropical forest ungulates, ranging from 10s to 100s km² (de Almeida Jácomo et al., 2013; Carrillo, Saenz, & Fuller, 2002; Fragoso, 1998; Jorge, Keuroghlian, Bradham, Oshima, & Ribeiro, 2019; Keuroghlian, Andrade Santos, & Eaton, 2015; Keuroghlian, Eaton, & Longland, 2004; Reyna-Hurtado, Rojas-flores, & Tanner, 2009). Finally, WLPs have long-lasting effects on forest dynamics. Through seed dispersal (Keuroghlian & Eaton, 2009), seed and seedling predation (Beck, 2006; Keuroghlian & Eaton, 2009; Silman, Terborgh, & Kiltie, 2003), soil and vegetation uprooting (Beck, Thebpanya, & Filiaggi, 2010; Keuroghlian & Eaton, 2009), and nutrient deposition, they disperse seeds and transport nutrients, and affect the physical, chemical, and biological

characteristics of the soil and forest understory (Barnes, 2018; Beck, Snodgrass, & Thebpanya, 2013; Villar et al., 2020). WLPs are highly sensitive to habitat loss and hunting, and as a result have become regionally extinct from much of their historical range (Altrichter et al., 2012; Thornton et al., 2020), resulting in them currently listed as “Vulnerable” by the IUCN Red List (Keuroghlian et al., 2013). Yet, in some agricultural regions, where pastures and soybean/corn plantations are rapidly replacing forest, WLPs seem to be in relatively high abundances (Lima et al., 2019).

The few studies and anecdotal reports about WLP habitat use in agricultural landscapes are contradictory. In an isolated, protected area surrounded by coffee plantation in Southeast Brazil, WLPs are restricted to the forest patch (Keuroghlian et al., 2004). Yet, in another isolated area of Central Brazil that is surrounded by corn plantations, WLPs readily use the matrix and have become a local nuisance (de Almeida Jácomo et al., 2013). Finally, in the Brazilian agricultural frontier, at the borders of the Amazonian forest, anecdotal information reports that WLPs come out of the forest to raid the corn crops (Lima et al., 2019). Nevertheless, until now, there has not been a comprehensive and systematic study to address to what extent WLP herds use and cross the matrix in agricultural areas.

We predict that if forests are essential for food, shelter, and displacement (here defined as the change in location between two points in time), WLP herds should only be found in the largest, most connected forest fragments, and there should be selection for both, forest cover and forest connectivity (Figure 1a). However, if forests are essential for WLP daily activities (such as food and shelter), yet matrix habitats are readily crossed, forest connectivity should not be a limiting factor, and herds should be found in large and small forest fragments alike, and there should be selection for forest cover, but not connectivity (Figure 1b). Finally, if forest is not essential for either food, shelter or displacement, herds should be found in forest and matrix coincident with their availability in the landscape; and there should be no selection for either cover or connectivity (Figure 1c). Our study allows for a more comprehensive understanding of the effects of forest loss and fragmentation, and increased availability of matrix habitat, on displacement and habitat use of this key Neotropical forest ungulate. More generally, this study will ultimately help address inquiries as to the ideal amount and configuration of remaining tropical forests in agricultural lands to ensure long-term native ungulate persistence and continued forest self-sustainability.

2 | MATERIALS AND METHODS

2.1 | Study areas

The study areas are located in the upper Paraguay River basin of Southwest Brazil, between 23°22 and 23°23 latitude south, 45°33 and 45°32 longitude west (Figure 2a). This region encompasses two municipalities that are part of the Cerrado Highlands and border the Pantanal floodplain to the East and South (Figure 2b). The 3,000-km²

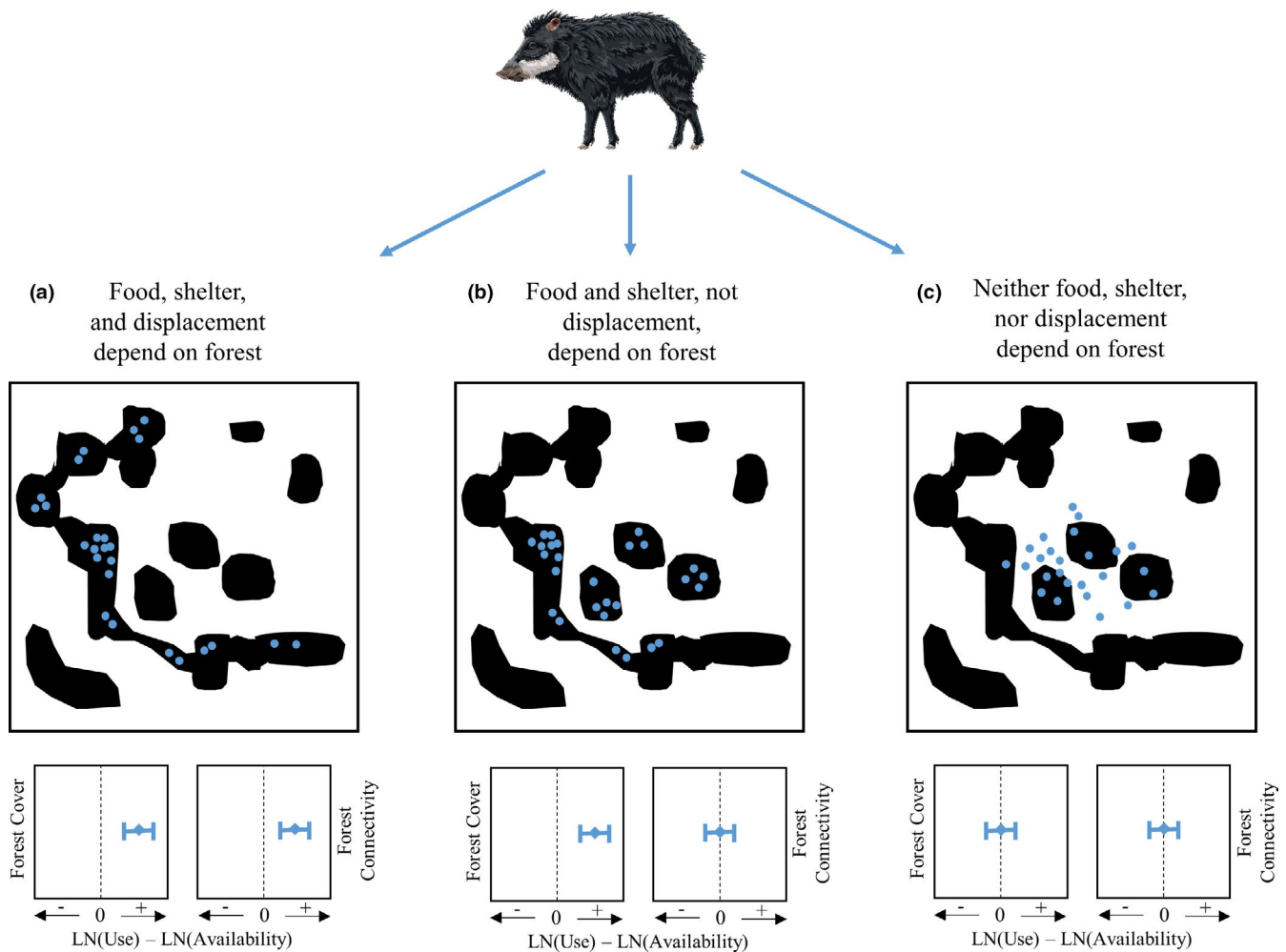


FIGURE 1 Predictions of the effects of forest loss and fragmentation on white-lipped peccary's (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla) use and displacement across the landscape. (a) If forest is important for food, shelter, and displacement, herds should only be found in the largest, most connected forest fragments, and there should be selection for both, forest cover and connectivity; (b) if forest is important for food, and shelter, but herds easily cross matrix habitats, herds should be found in large and small forest fragments alike, and there should be selection for forest cover, but not forest connectivity; finally, (c) if forest is not important for either food, shelter, or displacement, herds should be found in forest and matrix depending on their availability in the landscape, and there should not be selection for either cover or connectivity

Eastern Highlands (hereafter called *Corguinho* after the name of the township) occur in the Maracaju mountain ridge and encompass the headwater stream basins of the Negro, Taboco, and Aquidauana rivers, which supply water to the southern Pantanal floodplain. Native vegetation in this region consists of several types of seasonal savanna and semi-deciduous forest formations with high plant species diversity and endemism, including unique habitats like swamps dominated by a palm tree, *Mauritia flexuosa* (locally called buritizais), that are characteristic of headwater springs and small streams. Rapid agricultural expansion characterized by extensive conversion of natural vegetation to planted pasture (exotic grass monocultures) has relegated the original vegetation cover to approximately one third of its original area (Santana, 2015). The 10,000-km² Southern Highlands (hereafter called *Bodoquena*) occur in the Bodoquena mountain ridge, encompass the headwater streams of the Miranda river basin, and border the southern edge of the Pantanal floodplain (Figure 2b). Bodoquena vegetation

includes both deciduous and semi-deciduous seasonal savanna forests, with plant composition influenced by the neighboring Atlantic Forest biome (Pott & Pott, 2003). Similar to other Cerrado regions, forests of Bodoquena that are not federally protected, have lost some of the original vegetation due to land conversion for cattle-ranching and, more recently, monoculture expansion, such as soybean and corn plantations, as well as mining (Silva, 2008). Yet, the proportion of remaining forest in Bodoquena is slightly higher than that of Corguinho (which is 33%), at about 55%.

The climate of both regions is humid to subhumid, and tropical sub-warm, according to the Köppen classification (Köppen, 1884), with medium annual temperatures between 22°C and 26°C and maximum temperatures around 35°C to 40°C. Annual rainfall ranges from 1,500 to 1,750 mm, with a wet season occurring between October and April, and a dry season ranging from May and September (SEMAC, 2011).

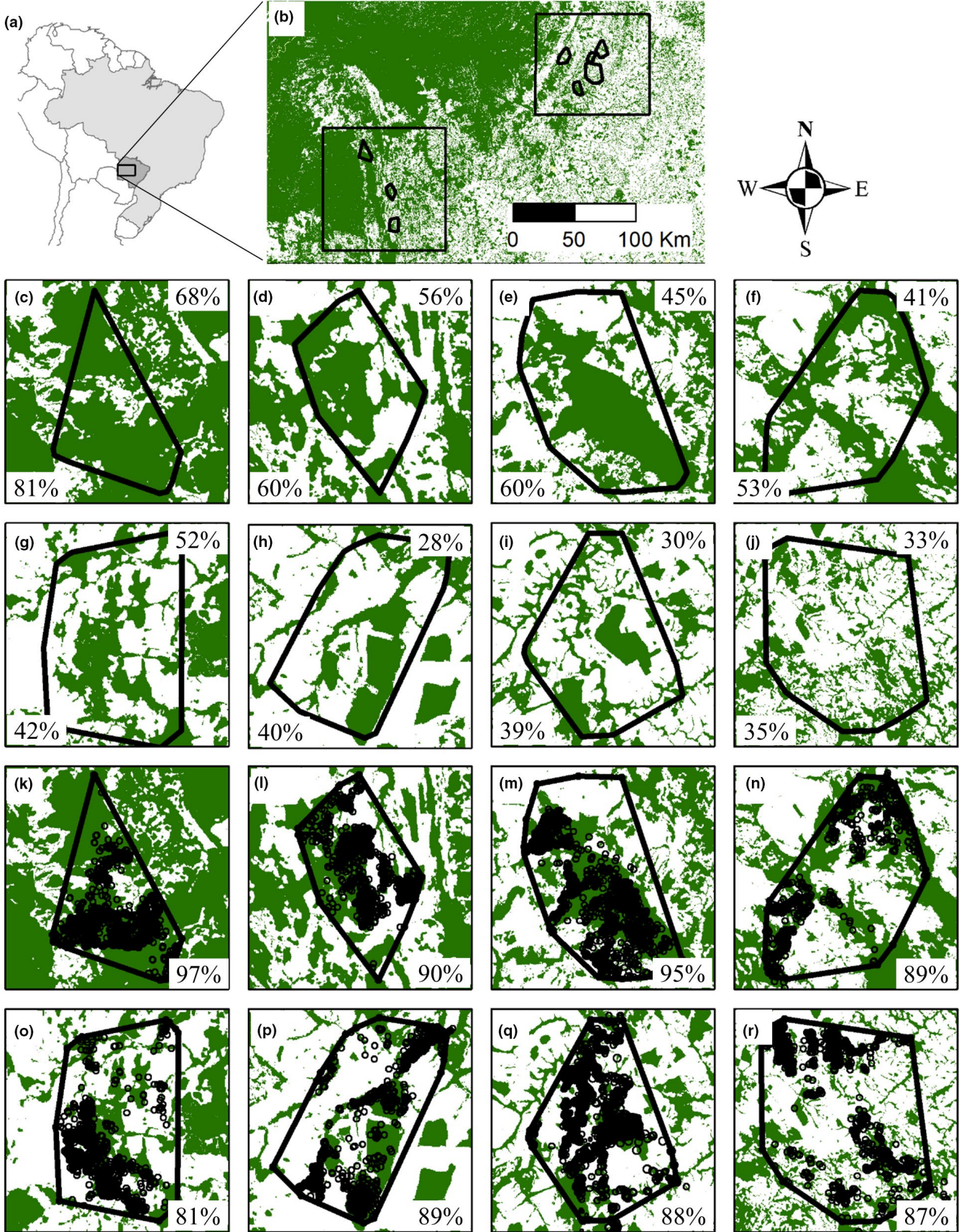


FIGURE 2 Home ranges and locations of eight white-lipped peccary herds (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla) tracked with GPS collars from 2013 to 2019. (a) General location of the study region within South America; (b) Study areas (Corguinho – Northeast; Bodoquena – Southwest) and home-range boundaries within study areas; (c–j) home ranges of each of the herds within the landscape: number on the top-right refers to the percent forest in the landscape, and number on the bottom-left refers to the percent forest within the home range; (k–r) locations of each herd within their home ranges: number on the bottom-right refers to the percentage of locations found in forest. Corguinho area (Northeast) has approximately 33% of native forest cover whereas Bodoquena area (Southwest) has 68% of native forest cover, if Bodoquena National Park and Kadiweu Indigenous Area are included (West, Figure 2b), and 56% when those are excluded

2.2 | Capture and handling procedures

Between 2013 and 2019, we captured WLPs in wired panel traps baited with fresh native fruit, corn and salt (SISBIO permits n. 31,088 and 46,131). Captured animals were sedated with an intramuscular injection of 0.9 ml/10 kg Tiletamine Hydrochloride and Zolazepam Hydrochloride (Zoletil 50®, Virbac, Brazil), using an air-compressed gun. Once sedated, we took morphometric measures of the animals, including body length and weight. We also collected blood samples and subcutaneously implanted tiny identification tags (microchips – Biomark®) in between the shoulder blades of each animal. All handling and measuring procedures followed guidelines described by Keuroghlian and Desbiez (2010) as well as guidelines from the American Society of Mammalogists (Sikes & Gannon, 2011). We gave each animal a unique name to facilitate easy reference. We estimated the age of each individual through tooth development and a qualitative analysis of tooth wear, following guidelines described by Keuroghlian and Desbiez (2010). We deployed GPS collars (Followit®, model Tellus Small Iridium, and Telonics®, model TGW-4470) on one or two of the healthiest adults captured, preferably one male and one female per herd, whenever possible. To allow for full recovery and ensure sedatives had worn off, we released the animals six to twelve hours after sedation. Follow-up monitoring confirmed that all animals rejoined their herds shortly after release. GPS collars recorded relocation data every three to six hours and sent the information to a web server every two to three days via two-way satellite communication (Iridium®). Collars collected data until they stopped communicating.

2.3 | Landscape metrics

We used two landscape metrics to test for forest selection: forest cover and forest connectivity. Maps from which we extracted values were generated from a 30-m resolution supervised land-cover classification of the State of Mato Grosso do Sul, Brazil (Reynolds, Wesson, Desbiez, Ochoa-Quintero, & Leimgruber, 2016) cropped to our study areas (Corguinho and Bodoquena).

To generate the layer of forest cover, we reclassified the original land-cover map (Reynolds et al., 2016) into two categories—forest and matrix—the first referring to the native forested area, and the latter to pasture and agriculture. It was possible to use this simplified categorization because within our study areas, native habitats are

mostly composed of native forest vegetation (sensu Oliveira-Filho & Ratter, 2002) and matrix habitats are mostly composed of pasture, and to a lesser extent, crops. We decided not to separate the matrix into pasture and crops, because in both study regions, the matrix was dominated by pasture. Only for one herd (in the southern part of Bodoquena), annual crops were part of the matrix, preventing us from statistically testing for distinct effects of matrix type in this study.

To generate the forest connectivity layer, we aggregated all forest pixels that neighbored another forest pixel (including diagonals) and generated individually identified blocks of connected forest (forest fragments). We then calculated the area of each forest fragment (in square-meters) and log-transformed (base 10) the area values, to emphasize changes in orders of magnitude. Lastly, we generated a raster layer in which each pixel within a given forest fragment received a value referring to the \log_{10} of area (in square-meters) of the forest fragment in which the pixel was embedded in. Thus, pixels within more connected forest fragments had larger values. This procedure created a raster for which each pixel referred to a \log_{10} -transformed forest fragment size, and it reflected the forest structural connectivity within the landscape (Jorge et al., 2013; Martensen, Pimentel, & Metzger, 2008; and Metzger et al., 2009). Both layers were generated with ArcGIS 10.2.1 (ESRI ©).

2.4 | Landscape and home-range boundaries

To test selection at two spatially explicitly hierarchical levels (landscape and home range, sensu Johnson, 1980), we determined each herds' home-range and landscape boundaries (Figure 2c–j). For home-range boundaries, we first considered individuals as being from the same herd when they overlapped more than 70% of their locations, or when previous VHF tracking data indicated that the area covered by neighboring tracked individuals was in fact used by the same herd over several years (data provided by Project Peccary). We acknowledge that our criteria for herd definition may have been somewhat arbitrary for three herds in Corguinho, which were very close together (Figure 2b). Nevertheless, individuals from each herd that were concomitantly monitored never overlapped locations, supporting our assumption that, for the time frame of our study, those can be defined as distinct herds.

Once each herd was determined, we defined a herd's home-range boundaries with the Minimum Convex Polygon (MCP) method

(Mohr, 1947). We chose the MCP because it is a direct, non-probabilistic method, and we were exclusively interested in defining boundaries, and not probability of low and high use. We reasoned that probabilistic methods are dependent on a series of parameter choices that could bias estimates and possibly make home range boundaries from distinct herds not directly comparable (Harris et al., 1990). We used a boundary that included all points (MCP 100) because we wanted to be the most inclusive in terms of area occupied by the herd. We calculated home range with the AdehabitatHR package (Calenge, 2015) in R, version 3.5.1.

For the landscape boundaries, we calculated an independent landscape area for each herd to ensure that the area represented what was available to the herd within its surroundings, as it could be slightly different for each herd. We chose the borders of each landscape as the south–north and east–west lines that were 10 km away from the outermost herd locations at east, west, north, and south. We used a distance of 10 km because previous analysis showed that the longest distance a herd covers in a 30-day period (long-term displacement) is 9.2 km (Jorge et al., 2019). Therefore, we believe that a distance of 10 km is representative of the potential maximum long-term displacement of the herd to the surrounding landscape.

2.5 | Statistical analyses of selection

We used compositional analysis (Aebischer, Robertson, & Kenward, 1993) applied to landscape metrics to test for non-random use of forest cover and connectivity. Compositional analysis considers non-random use of one habitat relative to the non-random use of another habitat. For forest cover, our two habitat categories were forest and matrix (the binary choice is explained at section 2.3). For forest connectivity, we classified fragments in one of two size classes: smaller or larger than 10 km². We used two classes because of our reduced number of herds ($N = 8$), as using more classes would make sample sizes for each category too small, and not statistically robust. We chose 10 km² as our cutoff size since it represents the smallest order of magnitude of WLP home ranges in continuous forests. Since home ranges are defined by squared values, we believe that categories of values are better represented by orders of magnitude (e.g., 1 km²; 10 km²; 100 km²) rather than linear values. Previous studies have shown that WLP herds of ~30–50 individuals have home ranges ranging from ~15 to 80 km² (Carrillo et al., 2002; Fragoso, 1998; Keuroghlian et al., 2004, 2015; Reyna-Hurtado et al., 2009). Therefore, we used the order of magnitude of 10 km² to represent a category of fragment size that herds would be selecting if they prefer to use connected forest. As such, use of fragments smaller than 10 km² could suggest that herds are not greatly affected by forest connectivity and are willing to cross the matrix to reach resource patches in isolated forest fragments, whereas preferential use of fragments of 10 km² or larger could suggest that herds prefer to use more connected forest.

To generate values of use and availability at the landscape level, we counted the number of pixels for each category (forest vs. matrix, and forests smaller vs. larger than 10 km²) within herds' home ranges for use, and compared the pixel counts within each herd's home range to the number of pixels for each category within each herd's landscape, which represented availability (Figure 2c–j). To generate values of use and availability at the home-range level, we counted the number of the locations within each category for all tracked individuals of one herd, to represent use, and counted the number of pixels for each category within each herd's home range, to represent availability (Figure 2k–r).

To test for non-random use of forest, we performed compositional analyses (Aebischer et al., 1993) with the package AdehabitatHS for R (Calenge, 2011) with the “randomization” option, 10,000 replications, and one as the number replacing zero values occurring in “used” ($r_{nv}=1$). Compositional analysis performs log-ratio transformations for values of use (in our study, GPS locations and pixel counts within home ranges), and availability (pixel counts within home ranges and landscapes) for forest cover ($\text{LN}(\text{forest}/\text{matrix})$) and forest connectivity ($\text{LN}(\text{larger than } 10 \text{ km}^2/\text{smaller than } 10 \text{ km}^2)$). After ratios are log-transformed, it calculates the difference between $\text{LN}(\text{use})$ and $\text{LN}(\text{availability})$ as the measure of non-random use. Finally, to test for the significance of the log-ratio differences ($\text{LN}(\text{use}) - \text{LN}(\text{availability})$), it uses a generalized likelihood ratio statistics (Λ), which is a multivariate analysis of log-ratios. The quantity $-N \ln(\Lambda)$, where N is sample size, fits a χ^2 distribution, which is used to accept or reject the null hypothesis (“use similar to availability”). We chose $\alpha = .05$ as our significance level. The degrees-of-freedom for each test was equal to one because there were only two categories for each fragmentation metric (forest versus matrix, and smaller versus larger than 10 km²). For further details of compositional analysis and Λ statistics calculation refer to Aebischer et al. (1993).

2.6 | Number of forest fragments used and percent of matrix crossing

To further evaluate whether individuals were crossing the matrix, we used the layer of individually identified isolated blocks of forest (see section 2.3) and assigned a fragment ID number to each GPS location. We then quantified how many consecutive locations were within the same forest fragment and how many were between two distinct forest fragments, for each herd.

3 | RESULTS

Over the course of six years (2013–2019), we tracked eight herds (13 individuals) and accumulated 14,460 GPS locations (Table 1). The number of days tracked per herd ranged from 107 to 560, and the number of months from 4 to 19, with an average of 347 days, or 12 months, per herd (Tables 1 and 2).

3.1 | Forest cover: use versus availability at the landscape and home-range levels

Percent forest cover in the landscapes where herds lived ranged from 28% to 68%, with a median of 43% (Figure 2c–j; $N = 8$). Percent forest cover within home-range boundaries ranged from 35% to 81%, with a median of 47% (Figure 2c–j; $N = 8$). Finally, percentage of GPS locations under forest cover ranged from 81% to 97%, with a median of 89% (Figure 2k–r; $N = 8$). Compositional analysis revealed that forest use was statistically significant with respect to availability at both hierarchical levels, yet with a much stronger selection at the home-range level (landscape: $\Lambda = 0.52$; $df = 1$, $p = .045$; home range: $\Lambda = 0.02$; $df = 1$, $p = .008$; Figure 3a).

3.2 | Forest connectivity: use versus availability at the landscape and home-range levels

On average, 73% of the landscape was covered by native forest fragments larger than 10 km² (range = 47% to 97%, $N = 8$), whereas within herds' home ranges, 84% of the area covered by forest fragments larger than 10 km² (range = 54% to 99%, $N = 8$), and 83% of the GPS locations were in forest fragments larger than 10 km² (range = 21% to 100%, $N = 8$). Compositional analyses revealed that at the landscape level, use of more connected forest was significantly higher than availability ($\Lambda = 0.51$; $df = 1$, $p = .04$; Figure 3b),

whereas at the home-range level, use of more connected forest was not significantly distinct from availability ($\Lambda = 0.64$; $df = 1$, $p = .07$; Figure 3b).

3.3 | Number of forest fragments used and percent of matrix crossing

Herds used one to 36 forest fragments within their home ranges. Herds occurring in areas with less forest cover were found in significantly higher number of forest fragments than herds occurring in more forested landscapes (Spearman Correlation Test: $S = 155.43$, $\rho = -0.85$, $p = .007$). Nevertheless, when 90% of the locations were considered, five of the eight herds used only one forest fragment, three used three fragments, and only one herd used 10 fragments (Table 2). Additionally, more than 90% of consecutive locations were within the same forest fragment for seven of the eight herds (Table 2).

4 | DISCUSSION

In a Neotropical rural landscape dominated by cattle-ranching and, to a lesser extent, crop plantations, the largest herd-forming and widest-ranging native ungulate of the Neotropics, the white-lipped peccary (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla;

TABLE 1 Summary information for eight white-lipped peccary herds (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla) GPS-tracked in two areas of Southwest Brazil, in Mato Grosso do Sul State, between 2013 and 2019

| Region | Herd name | Individual name | Gender | Start date | End date | N. days tracked | N. months tracked | Interval btn consecutive locations (hours) | N. locations | ~Locations/month |
|---------------|----------------|-------------------|--------|------------|----------|-----------------|-------------------|--|--------------|------------------|
| Bodoquena | Primavera | Primavera | Female | 02/24/17 | 09/07/18 | 560 | 19 | 6 | 1,864 | 100 |
| Bodoquena | Cachoeira | Cintia | Female | 10/26/16 | 11/27/17 | 397 | 13 | 6 | 1,446 | 109 |
| Bodoquena | Novo Horizonte | Leo | Male | 04/21/18 | 06/17/19 | 422 | 14 | 6 | 1,332 | 95 |
| Corguinho | Jacobina | Tainara | Female | 03/10/15 | 12/14/15 | 279 | 9 | 4 ^b | 1,642 | 177 |
| Corguinho | Jacobina | Cleide | Female | 03/10/15 | 10/18/15 | 222 | 7 | 3 | 1,759 | 238 |
| Corguinho | Colorado | Jay | Male | 07/12/13 | 10/27/13 | 107 | 4 | 6 | 377 | 106 |
| Corguinho | Colorado | Lurdes | Female | 06/05/14 | 12/12/14 | 190 | 6 | 6 | 452 | 71 |
| Corguinho | Taboco | Vagner | Male | 02/18/16 | 07/14/16 | 147 | 5 | 3 | 1,151 | 235 |
| Corguinho | Safira | Tony | Male | 06/08/14 | 10/21/14 | 135 | 5 | 6 | 395 | 88 |
| Corguinho | Safira | Malu ^a | Female | 06/08/14 | 11/24/14 | 169 | 6 | 6 | 504 | 89 |
| Corguinho | Safira | Malu ^a | Female | 10/01/15 | 01/03/16 | 94 | 3 | 3 | 732 | 234 |
| Corguinho | Safira | Cida | Female | 12/18/15 | 05/30/16 | 164 | 5 | 3 | 1,292 | 236 |
| Corguinho | Sta Tereza | Julia | Female | 07/27/14 | 11/15/14 | 111 | 4 | 6 | 349 | 94 |
| Corguinho | Sta Tereza | Valentina | Female | 08/09/15 | 01/05/16 | 149 | 5 | 3 | 1,165 | 235 |
| Total/Average | | | | | | 242 | 8 | | 14,460 | 150 |

^aMalu was caught and monitored in two years (2014–2015), with a period of 10 months of no monitoring between them.

^bThere was a collar mal-function and the interval between consecutive locations switched to 4 hr on its own.

TABLE 2 Period sampled, tracking duration, % forest available in home range (HR), number of forest fragments available and used, and number and percentage of consecutive locations in same and distinct fragments, for eight white-lipped peccary herds (*Tayassu pecari* Link 1795, Tayassuidae, Cetartiodactyla) GPS-tracked in two areas of Southwest Brazil, in Mato Grosso do Sul State, between 2013 and 2019

| Region | Herd name | Years tracked | N. days tracked | N. months tracked | % forest in HR | N. fragments within HR | N. fragments used by herd | N. fragments with 90% locations | Consecutive locations in same fragment | Consecutive locations in two distinct fragments | Total locations | % to same | % to another |
|---------------|----------------|---------------|-----------------|-------------------|----------------|------------------------|---------------------------|---------------------------------|--|---|-----------------|-----------|--------------|
| Bodoquena | Primavera | 2017–2018 | 560 | 19 | 81 | 37 | 1 | 1 | 1,766 | 0 | 1,766 | 100 | 0 |
| Bodoquena | Cachoeira | 2016–2017 | 397 | 13 | 60 | 28 | 2 | 1 | 1,285 | 2 | 1,287 | 100 | 0 |
| Bodoquena | Novo Horizonte | 2018–2019 | 422 | 14 | 42 | 44 | 9 | 3 | 939 | 86 | 1,025 | 92 | 8 |
| Corguinho | Jacobina | 2015 | 279 | 10 | 60 | 139 | 7 | 1 | 3,190 | 45 | 3,235 | 99 | 1 |
| Corguinho | Colorado | 2013–2014 | 297 | 10 | 53 | 191 | 4 | 1 | 718 | 28 | 746 | 96 | 4 |
| Corguinho | Taboco | 2016 | 147 | 5 | 40 | 82 | 6 | 1 | 999 | 27 | 1,026 | 97 | 3 |
| Corguinho | Safira | 2014–2016 | 411 | 14 | 39 | 213 | 19 | 3 | 2,318 | 240 | 2,558 | 91 | 9 |
| Corguinho | Sta Tereza | 2014–2015 | 260 | 9 | 35 | 756 | 36 | 10 | 1,159 | 155 | 1,314 | 88 | 12 |
| Total/Average | | | 347 | 12 | | | | | 12,374 | 583 | 12,957 | 95 | 5 |

Note: Percent to same (% to same) is the percentage of consecutive locations in the same fragment, while percent to another (% to another) is the percentage of consecutive locations that occur in two distinct forest fragments.

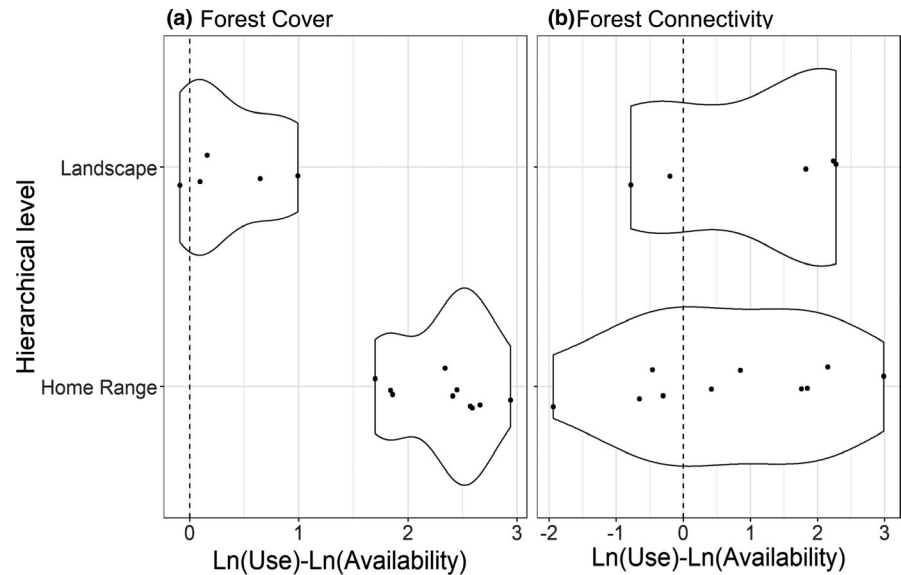
hereafter WLP), still consistently relies on the remaining forests for use and displacement. Previous studies have shown that WLPs are forest-dwellers (Carrillo et al., 2002; Reyna-hurtado et al., 2009). Yet, they were conducted in large continuous tracts of forests, whereas our results are the first to report that WLPs continue to be found under forest cover in agricultural landscapes, containing between 30% and 70% remaining forest.

Our results also highlight the importance of analyzing selection at more than one hierarchical level (sensu Johnson, 1980). In our study, selection for forest cover was not strongly depicted at the landscape level, with some of the herds occupying landscapes with reduced forest amount (~30%–40% Figure 2g–j). Yet, it was clearly depicted at the home-range level, with all herds having more than 80% of GPS locations found under forest cover (Figure 2k–r). Reyna-hurtado et al. (2009) found similar results when looking at two distinct hierarchical levels of their compositional analysis, with non-significant selection at the 2nd order of selection (home range vs. landscape) and a significant selection at the 3rd order of magnitude (locations within home range).

Forest connectivity, and not matrix crossing, explains how herds continue to be forest-dwellers, yet have their home ranges in areas with somewhat low forest cover (<50%). WLP selection for well-connected forests suggests that they need forest for both use and displacement. These may be related to foraging preferences, anti-predatory behavior (Lima & Bednekoff, 1999), and possibly thermoregulation. Previous studies show that WLP diets encompass mainly fallen fruits from forest trees (Altrichter, Carrillo, Sáenz, & Fuller, 2001; Bodmer, 1990; Bradham et al., 2018; Cullen Jr, Bodmer, & Valladares-Padua, 2001; Galetti, Camargo, et al., 2015; Kiltie, 1981). Additionally, much of the remaining forest corridors that connect bulkier forest areas include palm swamps and gallery forests, which, in other regions, have been described to be some of the preferred habitats used by WLP for food resources (Keuroghlian & Eaton, 2008).

Pumas are present in our study areas and remain an active predator of WLPs. In addition, humans threaten WLPs through hunting, poaching, and habitat modification (Beck et al., 2017). Furthermore, species also respond to the ghost of predation past (Brown & Vincent, 1992), and such behavior can shape the landscape of fear with anachronic responses for generations after the removal of predators. Non-systematic field observations of WLPs herds in the open show that they always remain very close to forest edges, and at the slightest threat, individuals quickly move to the adjacent forest, with step-selection function analyses further supporting those observations (Oshima, 2019). This behavior has also been seen in other herding ungulates in response to predatory threats, such as woodland caribou (*Rangifer tarandus*) in Canada, which selected certain habitats to avoid predation by wolves (*Canis lupus* - Rettie & Messier, 2000). As for thermoregulation, WLPs have been known to make use of a variety of micro-environments to combat extremes of temperature (Donkin, 1985). WLPs may be combining displacement through forest to avoid higher exposure to predation and high temperatures, and foraging for their preferred food as they travel between patches.

FIGURE 3 Compositional analyses revealed that (a) there was a statistically significant selection for forest cover at the landscape level ($\Lambda = 0.52$; $df = 1$, $p = .045$), and a highly statistically significant selection for forest cover at the home-range level ($\Lambda = 0.02$; $df = 1$, $p = .008$). On the other hand, (b) there was statistically significant selection for forest connectivity at the landscape level ($\Lambda = 0.51$; $df = 1$, $p = .04$) but not at the home-range level ($\Lambda = 0.64$; $df = 1$, $p = .07$)



Our study also shows that most WLP herds restricted themselves to one or two forest fragments; only the herd in the most fragmented area used more than three forest fragments (Figure 2j). This suggests that herds actively avoid the matrix, which may be related to potential short-term and long-term negative individual and population effects, such as increased energetic spending, higher exposure to predation, and higher air temperatures. If continued fragmentation leads to increased matrix crossing in order for herds to access their preferred patches, such behavioral changes may have detrimental behavioral and population effects. Increased time crossing matrices may increase travel times, exposure to predation and to higher temperatures. Additionally, optimal foraging theory suggests that increased travel time may increase foraging time within patches (Charnov, 1976; Mitchell & Powell, 2012), which may also have negative effects on forest regeneration.

Our results are relevant for management of Neotropical agricultural landscapes and suggest that in landscapes with medium to low percentage of forest cover, WLP, and possibly other forest-dwellers, may only be able to persist if the remaining forests are well connected. The importance of forest cover and connectivity to the presence of native mammals in fragmented landscapes is a well-researched topic. For example, Thornton, Branch, and Sunquist (2011) showed that some medium and large mammals of a fragmented landscape in Guatemala responded negatively to habitat loss and fragmentation, as did García-Marmolejo et al. (2013) in Eastern Mexico and Beca et al. (2017) in Southeastern Brazil. At a larger spatial scale, Jorge et al. (2013) revealed that in the Brazilian Atlantic forest, forest structural connectivity was the most important variable to predict habitat suitability for three of the largest Neotropical mammalian species: tapirs, jaguars, and white-lipped peccaries.

However, using high-resolution GPS data, we were able to show that forest connectivity directly affects the displacement of a large mammal through a fragmented landscape. To the best of our knowledge, only one previous study indicated similar patterns for a carnivorous social species, the bush dog (*Speothos venaticus*, Carnivora).

Through a combination of GPS and VHF tracking, Lima, Jorge, Jorge, and Morato (2015) showed that a family of bush dogs found in a landscape with 30% of forest cover restricted themselves to strips of gallery forests.

In summary, a native wide-ranging forest ungulate and key player in Neotropical forest dynamics still occur in agricultural landscapes with various amounts of native forest remaining, possibly because forest connectivity in those landscapes is still considerably high and therefore individuals can continue to move through and use forest resources. Long-term wildlife monitoring through camera trapping in the same regions corroborates our findings, concluding that WLPs do not occupy forest patches smaller than 20 km² (Keuroghlian, Eaton, Bradham, Oshima, & Jorge, 2017). Our results support that increased levels of forest fragmentation may prevent this native forest ungulate from persisting in agricultural lands, ultimately causing local and regional extinction of the species, which would cause unpredictable cascading effects to the remaining forested ecosystems. Our findings also suggest that conservation plans with the intent of long-term persistence of the full assemblage of medium and large native mammals need to actively promote forest connectivity to allow displacement, and ultimately long-term persistence, of more sensitive forest-dwelling mammals, such as the WLP, in fragmented landscapes.

ACKNOWLEDGEMENTS

We thank Paulino Oliveira Ângelo, Maria do Carmo Andrade Santos, Renata Reinoso Rocha, Bruna A., da Silva Andrade, Edivaldo O. de Souza and Marcello Schiavo Nardi (our project veterinarian) for assistance capturing, collaring, and monitoring white-lipped peccaries. We also thank all the volunteers that participated on the project, especially instructors Jeff Wilford and Liz Kinzly, the Global Ecotours & Expeditions volunteers, and Chatam University. We also extend our gratitude to Biofaces/Leonardo Avelino Duarte for their support. We acknowledge and appreciate the support from the local communities at Corguinho, Bodoquena, and Bonito for access to

land and key information regarding the local flora and fauna. We would also like to thank two anonymous reviewers for their thoughtful suggestions, which greatly improved the quality of this article. This research was funded by FAPESP (MCR: grant n. 2013/50421-2 and JEFO: 2014/23132-2), CNPq (MCR: grant n. 312045/2013-1; 312292/2016-3; JEFO: scholarship: 161089/2014-3), Silicon Valley Community Foundation, The Overbrook Foundation, the International ReSource Award, WCS Brasil, and Vanderbilt University. MCR was also funded by PROCAD/CAPES (project # 88881.068425/2014-01).

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4qrfj6q82> (Jorge, Bradham, Keuroghlian, Oshima, & Ribeiro, 2020) and Movebank.org.

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How to cite this article: Jorge MLSP, Bradham JL, Keuroghlian A, Oshima JEF, Ribeiro MC. Permeability of Neotropical agricultural lands to a key native ungulate—Are well-connected forests important?. *Biotropica*. 2020;00:1–12. <https://doi.org/10.1111/btp.12861>