Predator-Prey movement interactions: jaguars and peccaries in the spotlight

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Abstract

Landscape influences on predator-prey dynamics are critical for conservation. This study analyzed jaguar and white-lipped peccary interactions, revealing uncommon close distances and prevalent 3-5 km ranges, especially away from grasslands. Low peccary densities increased interactions. Findings inform conservation strategies, highlighting landscape structure and prey density roles in maintaining Pantanal's balance.

Keywords: carnivores, ungulates, forest edge, dynamics, Pantanal, landscape structure, conservation, spatial-temporal dynamics, *Tayassu pecari*, *Panthera onca*

1.- INTRODUCTION

Predator-prey interactions, a cornerstone of ecological systems, significantly impact population dynamics (Schmitz, 2005; Creel & Christianson, 2008). The landscape structure is crucial in facilitating these interactions, providing opportunities for successful hunting for large carnivores and predator avoidance strategies for the prey (Schmitz et al., 2017; Smith et al., 2019; Suraci et al., 2022). Understanding how landscape structure influences predator-prey interactions is vital for conservation programs (Creel & Christianson, 2008).

Large tropical carnivores in changing habitats exhibit diverse prey preferences and employ various hunting strategies influenced by prey type and landscape structure (Fernández-Sepúlveda & Martín, 2022; Gaynor et al., 2019). These interactions, shaped by factors like scent, vision, and animal density, are complex to measure (Smith et al., 2019; Potts et al., 2014). Investigating them is challenging due to the hierarchical nature of predation sequences and species-specific behaviors (Suraci et al., 2022), with studies often relying on temporal activity patterns and overlapping home ranges from camera traps, though obtaining detailed movement data is costly and logistically difficult.

The Pantanal is renowned for its biodiversity, including carnivores like jaguars (*Panthera onca*, e.g., Alegre et al., 2023; Morato et al., 2018) and prey such as white-lipped peccaries

(Tayassu *pecari*, e.g., Keuroghlian et al., 2004; Oshima, 2019). Jaguars exhibit dietary flexibility, preying on various species based on availability (e.g., marine turtles in Costa Rica; Carillo et al., 2009; Middleton et al., 2021). In the southern Pantanal, the three most frequent prey items registered for jaguars were cattle, caiman, and white-lipped peccary (Cavalcanti & Gese, 2010; Perilli et al., 2016) hereafter WLP.

Interactions between jaguars and WLP in the Pantanal involve jaguars' predation, defensive mobbing, and attacks on individual jaguars by peccary herds (Rampim et al., 2020). However, fine spatial-temporal resolution data on where and when those interactions occur are scarce. This study aimed to determine if the landscape structure influences these interactions' spatial distribution and timing. We used the Dynamic Interaction Index (DII) to assess movement direction and speed and examined the distance between species over time to accomplish this. As the first study in this movement ecology context, our questions are exploratory: How are the interaction patterns between the jaguar and the WLP presented? At what distance are the movements of these interactions recorded (predator-prey), and in what period of the day do they occur? Finally, we are interested in understanding the spatial context of the DII between predator and prey. This study provided insights into the dynamics of jaguar-peccary interactions in the Pantanal, informing conservation strategies to preserve this delicate balance.

2.- METHODS

2.1. Jaguar and White-lipped peccary movement dataset

Jaguar movement data come from three individuals monitored between August 17th and September 30th, 2015 (GPS dataset, Morato et al., 2018). WLP movement data comes from five individuals GPS-tracked in the same period and sites of the jaguar dataset, with all individuals from each ranch belonging to the same herd, and different herds occupying separate ranches (Oshima, 2019). Both datasets come from the Southern Pantanal, Fazenda Barranco Alto (A, Figure 1), and Caiman Ecological Refuge (B, Figure 1). The data was collected during the dry season in the Pantanal.

2.2. Species interaction analysis

We analyzed all the locations where predator-prey moved synchronously through shared home range sections (Dryad Digital Repository). We had a dataset of 525 pairs (predator-prey) locations (Table A; Supporting Information - SI). To understand interaction dynamics, we applied the Dynamic Interaction Index (DII) developed by Long and Nelson (2013). This index measures how two animals move relative to each other over time, considering both their movement direction and distance between each step. Positive DII values indicate that the movements of both animals are more aligned or synchronized, suggesting attraction, while negative values mean their movements are less aligned or diverge, suggesting avoidance. Values close to zero represent random movement, indicating neither attraction nor avoidance. We also calculated the percentage of predator-prey (pair) locations that resulted in interactions using the pair DII results divided by the total synchronized locations.

Considering the DII's limitation regarding the absence of predator-prey distance evaluation, we computed the distance separating the two entities using the wildlifeDI package (Long et al., 2022) in R (R Core Team, 2022). No previous study has determined the distance a jaguar can spot a WLP (and vice versa). Since this distance can vary depending on the surrounding environment, we have decided to use a maximum distance of 5000 meters due to previous work showing jaguars interacting with their environment at this scale (e.g., Alvarenga et al., 2021; Alegre et al., 2023).

2.3. Model and environmental variables

We used generalized linear mixed-effect models (GLMM) to determine the effect of the landscape structure and predator and prey densities in which the interactions occurred. We coded the pairs of interactions (e.g., Sossego and Canela interaction were coded as "sc") as random variables using the glmmTMB package (Brooks et al., 2017) to carry out the model. We conducted diagnostic tests to assess the performance and validity of the models, including the KS, dispersion, and outlier tests, using the DHARMa package (Hartig, 2022).

We categorized the dependent variable of our model based on the DII results. The observations of the interaction between both species, such as attraction and avoidance, were assigned a value of 1. Any value greater than 0.4 and less than -0.4 would fall into this classification. Random data was assigned a value of 0. Although there is no specific study to establish these exact thresholds, we developed them as a methodological approach to objectively classify interactions based on directional and speed metrics, aligning with the general understanding that values closer to 1 indicate stronger interaction. The independent environmental variables were obtained from MapBiomas at a resolution of 30 m (MapBiomas project - 2015). We calculated the distance from the forest and grassland using the LSMetrics software (Niebuhr et al., 2020). We used these two variables because they are crucial in the habitat selection of both species (Alvarenga et al., 2021; Alegre et al., 2023; Oshima, 2019).

We used predator and prey density as independent variables in our model. To estimate the density of jaguars and WLPs, we performed a kernel density estimation for each species separately, using GPS data, with a 1000-meter radius and a pixel resolution of 30 meters, using QGIS 3.10.7-A Coruña (QGIS Development Team, 2020). The density estimates are derived directly from the movement data of the monitored individuals and not from a spatially explicit density of individuals per unit area. We also included individuals monitored with GPS who were not selected for the interaction analysis in the kernel density estimates (Table B, SI). Although the analysis focused on GPS-collared individuals, it is essential to note that we could not ensure the absence of uncollared individuals within the study area.

To create the predictive maps, we used rasters corresponding to each variable in the model. These rasters were resampled to ensure consistency in resolution and extent. After resampling, the rasters were stacked into a multi-layer dataset, allowing for the generation of predator-prey interaction predictions based on our GLMM model.

3.- RESULTS

We investigated predator-prey movement interactions between three jaguars (namely Esperança, Nusa, and Sossego) and five peccaries (Marcello, Roberta, Canela, Nanda, and Trina) with different home ranges (Figure 1). In 32 to 44 days, we observed six interactions in which attractions (positive) and avoidances (negative) were recorded from a total of 118 dynamic interactions index (sum of attraction, random, and avoidance behavior) (Figure A and Table A, SI). Nusa and Roberta had the highest DII proportion, 35.1%, followed by Esperança and Marcello (24,1%). The lower DII proportion was from Sossego and Trina, with 14.6 % (Table A, SI). The distance between predator-prey individuals exhibited considerable variability, with few interactions occurring within distances less than 700 meters between them (Figure B and Appendix A, SI), and distances within a range of 1 to 3 kilometers were prevalent.

Interactions within the 700-meter range mainly involved Sossego-Nanda, totaling five locations and one avoidance interaction (Table C, SI). Meanwhile, Nusa-Marcello had nine locations within this range, resulting in one avoidance and two attraction interactions. Interactions occurring within a distance of 700 meters were mostly during the twilight and night periods (Appendix A, SI).

3.1. The dynamics of interaction index in the landscape

Our DII model analysis revealed two significant variables: distance from grassland areas and WLP density. The results indicate that the probability of interaction increased with greater distance from the grassland areas ($\beta = 0.245$, $p < 0.01$) and lower density of peccaries ($\beta = -0.244$, $p < 0.01$). On the other hand, the effect of distance from the forest was not significant (Table D, SI). Although jaguar density was not statistically significant, a trend suggested that higher densities correlate with greater interaction (Figure 2). We also observed that the core areas of peccary home ranges showed a low probability of interaction. In contrast, edge zones where forest borders farming areas exhibited a higher probability of interaction (Figure 1). Our interaction dynamics model passed all diagnostic tests for accuracy and reliability (Figure C, SI)

When analyzing the distribution of distances between predators and prey, shorter distances occurred at the edge of the grassland areas (Figure D- A, SI). However, no pattern was observed between the density of WLP and the minimum distance at which they came in contact with predators (Figure D- B, SI).

4.- DISCUSSION

Studies on Neotropical predator-prey interactions face challenges as they depend arbitrarily on individual behaviors (Suraci et al., 2022). Our study recorded 32 to 44 days of overlap between predator and prey in time and space from GPS datasets. Furthermore, as far as we are concerned, this is the first exploration of these species movement interaction dynamics in the Neotropics, examining how landscape structure influences interactions.

Our results provide insights into predator-prey dynamics and identify key landscape features influencing interactions. We observed that grassland distances and prey density significantly affect interactions between jaguars and peccaries in the Pantanal. Conversely, contacts were predominantly recorded at shorter distances along the edges of grasslands during crepuscular and night periods (Figure A and Figure D, SI). Jaguars typically remain close to forest surroundings and venture deeper into grasslands only under medium to high levels of moonlight illumination (dos Santos et al., 2022).

Predator-prey interactions rely heavily on perceptual abilities (Creel & Christianson, 2008; Gaynor et al., 2019). The jaguar exhibits remarkable perceptual capacity, supported by evidence of interactions with the landscape on a large scale (Alegre et al., 2023; Alvarenga et al., 2021). In contrast, WLP form herds that allow them to alert each other and perceive large predators (Nogueira et al., 2017; Rampim et al., 2020). Most of the interactive dynamics between the two species have been ascertained, primarily at greater spatial distances. Conversely, close-distance interactions between jaguars and peccaries are infrequent and potentially indicative of a process of trophic degradation (Estes et al., 2011; Ripple et al., 2014). The loss of apex predators and their key prey can trigger significant changes in trophic interactions, altering ecosystems' structure and function. WLP population collapses have consistently been associated with reduced encounter rates via camera traps, evidencing decreased visibility and presence (Whitworth et al., 2022). This decrease in predator-prey interactions could indicate deeper alterations in ecological dynamics.

Furthermore, our findings identified that the distance from grassland areas plays a significant role in the interaction dynamics between jaguars and peccaries. Predators such as the jaguar prefer these transition zones between forest and grassland (Alegre et al., 2024; dos Santos et al. 2022), which may be related to vital activities such as prey hunting, as corroborated in our study. The interaction pattern suggests high density within WLP core home range areas may limit interactions. In contrast, the increased probability of interaction along forest edges near farming areas may result from some peccary individuals venturing into these zones in search of food resources (Jorge et al., 2019). Although farming was not a study focus due to its limited distribution, its presence may influence interaction dynamics by providing additional resources.

Finally, our findings reveal variability in predator-prey encounters, which could be influenced by physiological state, age, and experience (Gaynor et al., 2019; Suraci et al., 2022). These aspects can modulate the proximity of encounters and the movement dynamics during such interactions. In our data, we observed that at distances less than 700 meters, some high DII simultaneously show avoidance and attraction movement patterns. These patterns at shorter distances could indicate behaviors related to hunting by the jaguar or awareness from both species of the presence of each other, although these activities had not been directly observed.

We must recognize our study's limitations, including the low number of overlapping individuals. Additionally, the selected WLP belonged to the same herds within each study area despite individuals exhibiting fission-fusion social behavior, which could have influenced the variability of the observed interactions. Furthermore, the possible presence of other unmonitored predators and prey in the evaluated landscapes was not investigated and incorporated here.

Our findings highlight several key areas for future research, particularly focusing on the influence of farming areas on jaguar-peccary interactions. Long-term studies should be conducted to examine how changes in resource distribution and anthropogenic pressure, such as agricultural expansion, impact the behavioral dynamics of these species over time. Additionally, integrating advanced techniques such as biologging tags capable of recording physiological data and behaviors alongside GPS data would provide a more complete interpretation of these interactions, allowing researchers to capture nuanced behaviors and responses to environmental shifts in real-time.

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Data availability statement

The data supporting the findings of this study are openly available in the Dryad Digital Repository at: https://doi.org/10.5061/dryad.sqv9s4nc4.

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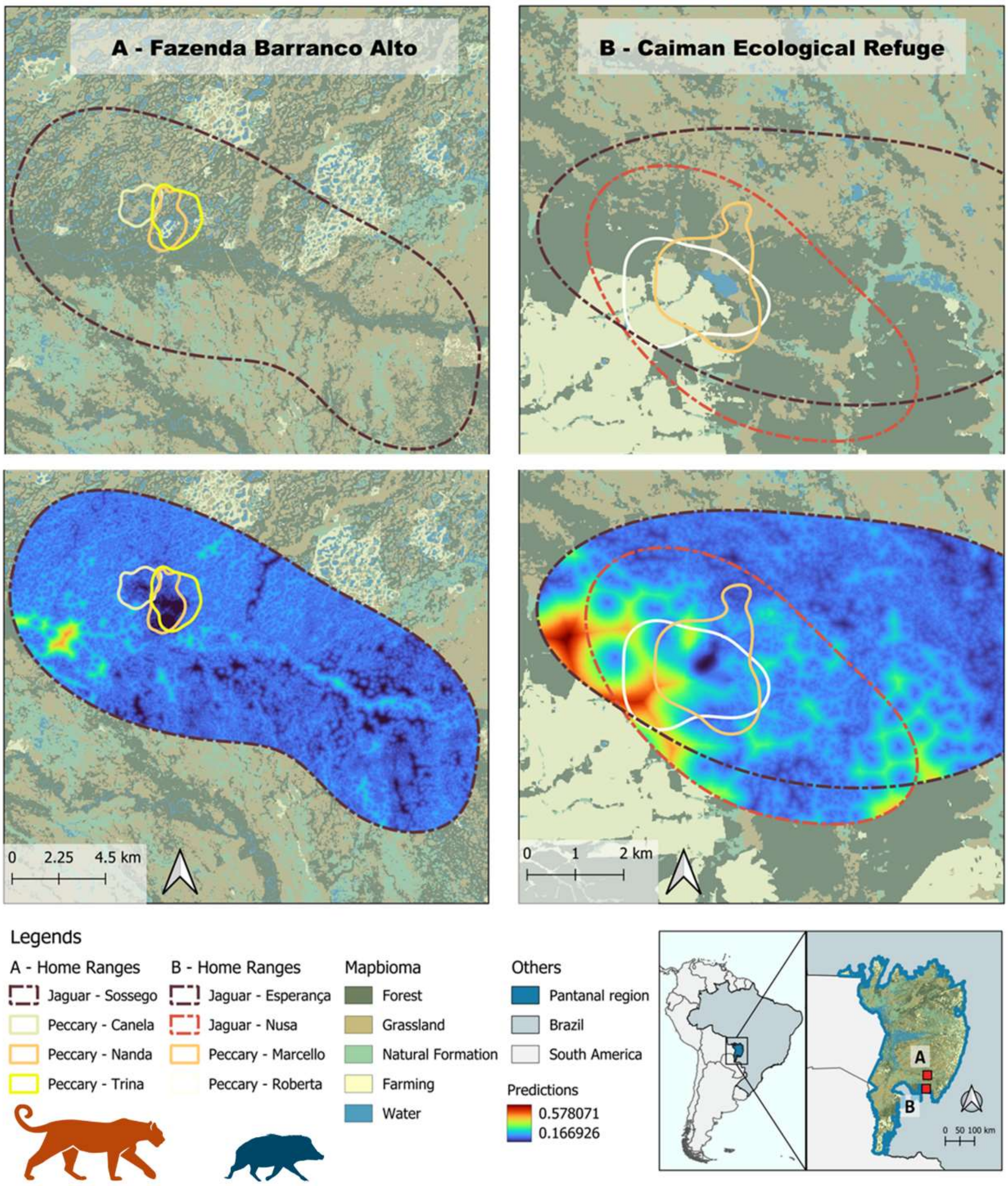

A - Fazenda Barranco Alto
B - Caiman Ecological Refuge
0 2.25 4.5 km
0 1 2 km
Legends
A - Home Ranges
Jaguar - Sossego
Peccary - Canela
Peccary - Nanda
Peccary - Trina
B - Home Ranges
Jaguar - Esperança
Jaguar - Nusa
Peccary - Marcello
Peccary - Roberta
Mapbioma
Forest
Grassland
Natural Formation
Farming
Water
Others
Pantanal region
Brazil
South America
Predictions
0.578071
0.166926
A
B
0 50 100 km

Figure 1: *Study areas where the interactions took place.* Top: A, Fazenda Barranco Alto. B, Caiman Ecological Refuge. Both areas are working ranches where ecotourism activities are developed and cattle ranching, managed with a free grazing system rotating within heterogeneous landscapes comprising natural formations, grassland, forest patches, and livestock-planted pastures (farming). Owners of both ranches support the conservation of wildlife and local research. Although both farms are in the southern Pantanal, the landscapes used by peccaries and jaguars in this study were slightly different, with areas surrounding Caiman being more modified for livestock non-natural pasture. In contrast, the landscape used by the animals in Fazenda Barranco Alto was surrounded by freshwater and salt lakes and had a higher percentage of forest cover. Inside the Caiman Ecological Refuge is a private protected reserve with 5,6 thousand ha, which is not used for tourism or cattle ranching. Bottom: Predictions of jaguar-peccary interactions within their ranges correspond to the study areas mentioned above. Warmer colors (red) indicate greater interaction probabilities, while cooler colors (blueish) signify areas with lower interaction probabilities.

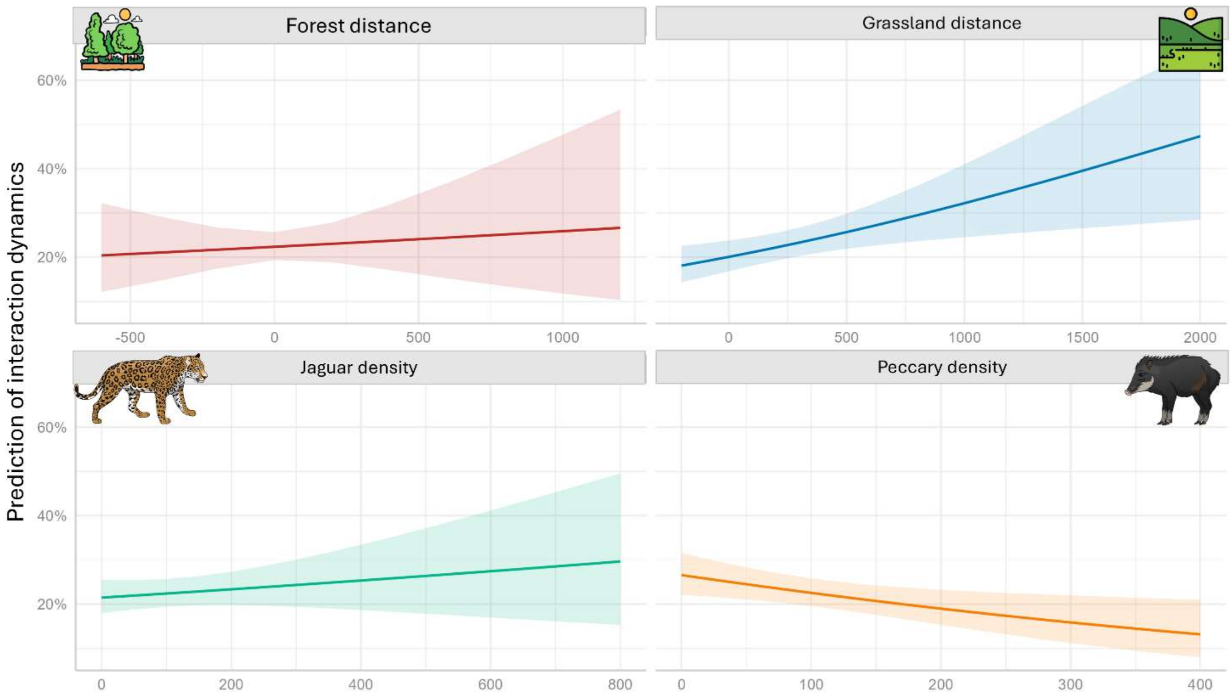

Figure 2: Prediction of the four variables explored using generalized linear mixed-effect models to test the predator-prey movement interaction. Distance from the forest and jaguar density were non-significant variables within the model, while distance from grassland and white-lipped peccary density.