
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E
BIODIVERSIDADE**

**ECOLOGIA DO MOVIMENTO E DINÂMICA ESPAÇO-TEMPORAL DA ONÇA-
PINTADA (*PANTHERA ONCA*) NO PANTANAL SUL DO BRASIL**

CLAUDIA ZUKERAN KANDA

Dissertação apresentada ao
Instituto de Biociências do Campus
de Rio Claro, Universidade
Estadual Paulista “Júlio de
Mesquita Filho”, como parte dos
requisitos para obtenção do título
de Mestre em Ecologia e
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Setembro - 2015

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Orientador: Dr. Milton Cezar Ribeiro

Co-orientador: Dr. Mauro Galetti

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2015

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Aos meus pais, Akemy e Claudio

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“What we know is a drop, what we don’t know is an ocean”

“No great discovery was ever made without a bold guess”

Isaac Newton

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Resumo

Todas as espécies vivas interagem entre si ou com outras espécies. A presença dos coespecíficos pode influenciar nos padrões de movimentos e determinar o uso do espaço de cada indivíduo. O uso do espaço emerge do processo de movimento dos indivíduos, sendo que as decisões de quando e para onde mover-se estão relacionadas com a seleção de ambientes que potencializem a localização de recursos e assim, favorecer em seu desenvolvimento, sobrevivência e sucesso reprodutivo. Os mamíferos restringem seus movimentos em habitats familiares e a seleção de habitats pode estar relacionada com as variações dentro do seu ciclo de atividades circadianas. A presença dos coespecíficos também pode desempenhar um fator importante na seleção do uso do espaço em mamíferos carnívoros, gerando respostas de atração em períodos de reprodução ou mesmo a de repulsão, com o propósito de minimizar encontros e diminuir as interferências diretas na obtenção de recursos. Desta forma, o presente estudo teve como objetivo testar e analisar os fatores determinantes no uso do espaço por onças-pintada (*Panthera onca*) no Pantanal do Brasil. Nós utilizamos a regressão condicional logística ajustada ao modelo de *Step Selection Functions* (SSF) para compreender como e quais fatores afetam o uso do espaço e assim, auxiliar no entendimento das necessidades biológicas e ecológicas para a sobrevivência das espécies. O comportamento de restringir seus movimentos dentro de sua área de vida foi estimado pela força de seleção em função da distância do centro da área de vida do indivíduo. Já a seleção do habitat ao longo do ciclo circadiano foi estimada pela força de seleção em função das horas do dia. A influência dos coespecíficos foi caracterizada por meio de um conjunto de dados de localizações simultâneas de indivíduos com áreas de vida sobrepostas e a resposta foi estimada pela força de seleção ao indivíduo mais próximo a cada passo de movimento. Os resultados indicam que o uso do espaço pelos organismos pode ser predito pela seleção de habitats favoráveis variando ao longo do ciclo circadiano, pela diferença sexual no comportamento de mover-se próximo ao centro de sua área de vida e pela dinâmica espaço-temporal de movimento dos coespecíficos.

Palavras-chave: sociabilidade, uso do espaço, carnívoro solitário, coespecífico, comportamento de movimento

Abstract

All living things interact with other conspecifics or with other species. The presence of conspecific can influence individual movement patterns and determine individual's space use. The space use emerges from individual movement process, and the decisions for when and where to move are related by habitat selection that enhance the location of resources for increase your fitness to growth, survival and reproduction. Mammals restrict its movements in familiar habitats and this selection can be associated to their circadian rhythm. In carnivores mammals the presence of near conspecifics can also be an important factor in the space use, as an attraction impulse for reproduction or a repulse action to minimize direct interference to get resources. This project aimed to analyze the determining factors in space use by jaguars (*Panthera onca*) in the Pantanal of Brazil. Conditional logistic regression was applied for adjusted Step Selection Functions (SSF) model to understand how and which factors affect space use. Homing behavior was estimated by selection strength in function for distance from the center of individual home range and habitat selection changing over circadian cycle was estimated by selection strength in function for day hours. The conspecific influence on movement was characterized using a set of data acquired simultaneously from animals tracking and individuals with contiguous home range. In addition, the presence of conspecific responses was estimated by the selection strength of nearest individual for movement at each steps. These results indicate that the space use by organisms is predicted by habitat selection along the circadian cycle, differences in the homing behavior between sexes and by spatial-temporal dynamic of conspecific movement.

Keywords: sociability, space use, solitary carnivore, conspecific, movement behavior

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1. Introdução geral

A ecologia de movimento têm como foco explicar processos ecológicos correlacionando os padrões de movimento (Nathan et al., 2008), pois processos como a invasão biológica, dispersão de sementes (Wright et al., 2008) e a dinâmica da comunidade (Damschen et al., 2008; Vanak et al., 2013) estão associados com o movimento animal. Os dados de movimento inseridos em seu contexto ambiental, permite explorar as causas dos fatores externos que regem os padrões de movimento, ajudando assim na compreensão das consequências do movimento nos processos ecológicos e evolutivos (Nathan et al., 2008).

Os mamíferos não se movem aleatoriamente na paisagem, mas exibem uma maior probabilidade de mover-se em direção a locais previamente visitados (Piper, 2011; Oliveira-Santos, 2013; Polansky, Kilian e Wittemyer, 2015). A qualidade do habitat e a presença de seus coespecíficos também podem determinar o uso do espaço, onde os animais devem estabelecer-se em habitats que ofereçam maior abundância de recursos, proteção e outras características que garantam seu desenvolvimento, sobrevivência ou a sua reprodução (Piper, 2011). A influência dos coespecíficos no uso do espaço pode ser predita por duas respostas comportamentais de movimento: (a) atração ao coespecífico como estratégia de encontrar recursos favoráveis durante o processo de seleção de habitat (Fletcher Junior, 2006; Zeigler et al., 2011) ou mesmo a formação de territórios como propósito de minimizar encontros com seus coespecíficos e (b) diminuir as interferências diretas na obtenção de recursos (Potts e Lewis, 2014).

Em carnívoros solitários, a alta sobreposição de área de vida intersexual (Cavalcante e Gese, 2009; Vidal et al., 2012; Elbroch, Quigley e Caragiulo, 2014; Rodgers et al., 2015) e entre machos (Cavalcante e Gese, 2009; Rodgers et al., 2015), assim como a alta proximidade de uso simultâneo do espaço entre fêmeas e fêmeas e entre machos e fêmeas (Elbroch, Quigley e Caragiulo, 2014) indicam um grau de convivência antes não relatada. A existência de um grau de tolerância à presença de seus coespecíficos também parece ocorrer em carnívoros solitários de grande porte como a onça-pintada (*Panthera onca*). Apesar desta espécie ser considerada de hábito solitário e os machos e as fêmeas encontram-se apenas no período reprodutivo (Silveira e Crawshaw Junior, 2008), a alta sobreposição nas áreas de vida entre machos e fêmeas e, entre machos assim como a alta

proximidade entre os seus coespecíficos (<200 m) sugerem a ausência de territorialidade (Cavalcanti e Gese, 2009).

A onça-pintada (*P. onca*) é considerada uma espécie importante no equilíbrio e na estruturação das comunidades tróficas por predação diversas espécies de grande e médio porte (Weckel, Giuliano e Silver, 2006; Porfírio, 2009). Mas apesar desta importância, a espécie encontra-se vulnerável ao risco de extinção em diversos biomas brasileiros (Tôres et al., 2008) por ser uma espécie ecologicamente exigente (De Angelo, Paviolo e Di Bitetti, 2011). Ao compreender os mecanismos comportamentais subjacentes na escolha da área de vida e como os animais movem-se e interagem com seus coespecíficos, pode tornar-se possível prever os efeitos da variação do habitat na estrutura espacial de uma população (Potts e Lewis, 2014), uma vez que a exclusão ou inclusão de um indivíduo pode afetar toda a dinâmica ecológica populacional.

Esta dissertação tem como objetivo testar e analisar os fatores determinantes no uso do espaço por onças-pintadas (*Panthera onca*) no Pantanal do Brasil. A nossa hipótese é de que o uso do espaço seja determinado pela seleção de habitats familiares e esta seleção variando ao longo do ciclo circadiano, assim como os movimentos é exercida pelas respostas comportamentais de atração ou repulsão aos seus coespecíficos dependentes do gênero sexual e da condição reprodutiva. Nossos resultados auxiliam na compreensão dos mecanismos determinantes no uso do espaço pelos animais e assim, indicar quais as necessidades biológicas e ecológicas para a espécie.

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3. Artigo

Importance of conspecifics on the movement pattern of a solitary carnivore, the jaguar (*Panthera onca*)

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Abstract

All living species interact with each other and with other species. The presence of conspecifics can influence patterns of movement and determine the space use by each individual. Space use emerges from the individual movement process and decisions of when and where to move are related to habitat selection that potentiate the acquisition of resources and, thus, influences survival and reproductive success. In carnivore mammals, the presence of near conspecifics can also be an important factor influencing the movement process, as either an attraction impulse for reproduction or a repulsive action to minimize direct interference to get resources. The present study aimed to analyze the determining factors, especially the effect of conspecifics, in space use by jaguars (*Panthera onca*) in the Pantanal of Brazil. We used Step Selection Functions (SSF) to evaluate the importance of ranging behavior, habitat selection along the time of day and distance of conspecifics (males and females) and, if there are differences between the sexes in each of these three factors on the jaguars' space use. The results indicate that incorporating the spatio-temporal dynamics of the movement of conspecifics and, also including the effects of ranging behavior differing between sexes and habitat selection varying through the day can be predict space use. Females presented a strong ranging behavior (tendency to moves anchored to home range center) while the male did not. Habitat selection change along the times of day, selecting forest and water bodies through the day, mainly at night. Male and females selected areas that maximized the likelihood of encountering female, but females avoided areas with likelihood of male encounters. Our findings reinforce the influence of landscape structure and dynamic on the fauna populations, in especial those that can be influenced by the presence or absence of conspecifics.

Keywords: space use, movement ecology, Pantanal, step selection function, dynamic interaction

Introduction

Space use emerges from the movement process performed by individuals [1]. Decisions of when and where to move are closely related to the selection of areas with potential resources [2-4]. Thus, an organism's movement can be influenced by external biotic factors (e.g. habitat [5-6], predators [7], competitors and conspecifics [1,8]) and abiotic factors (e.g. temperature [9] and the terrain [7]), as well as motivated by the individual's internal states (e.g. endogenous circadian rhythm [10]) [11]. According to these motivations the movements will be constrained by species-specific intrinsic features, such as their abilities of locomotion, orientation and cognition [11].

For most mammals, space use is not random; their movements are restricted to specific regions known as home ranges [12-15]. This restriction is an important factor in animals' decisions regarding their space use, as it suggests the tendency to move preferentially in familiar areas, which, in turn, can facilitate their success in survival and reproduction [16]. The selection of familiar areas is evidence of the cognitive capacity and spatial memory of individuals [14, 17-19], who use experiences gained in previous movements to enhance their effectiveness in finding the resources [2, 14, 16, 18] resulting in a more directional movement pattern.

The use of spatial information in their movement decisions also includes the perception of and response to their conspecifics, be that attraction or repulsion, according to environmental conditions [20] and their social and reproductive state. Territoriality seems to differ among sexes in rodents, as females tend to be less territorial in highly productive environments with high renewal rate for food and more homogeneous distribution of food resources; meanwhile, the determining factor for high territoriality among males is the spatial distribution of females [21].

Evidence obtained with rodents suggests that sex differentiates territoriality, as females tend toward low territoriality in highly productive environments with high renewal rate and/or a more homogeneous distribution of food resources; meanwhile, the determining factor for high territoriality among males is the localization of aggregated females [21].

For solitary carnivores, the absence of intersexual territoriality [15, 22-24], strong intersexual spatial association [25, 26], high overlap of home range among males [23, 24, 27], as well as a high proximity between their conspecifics in space use [23] indicate a degree of coexistence not previously reported. In addition, they may present a greater tolerance for the presence of genetically related individuals [24, 28].

Cavalcanti and Gese [23] tried to understand the spatial ecology and interactions of conspecific jaguars (*Panthera onca*) using a spatial and temporal approach; however, they did not analyze concurrent movement decisions of the individuals in space and time. To understand effects of the presence of conspecifics on the motion dynamics of jaguars, it is necessary to take into account information about sex and reproductive conditions, because this specie traditionally recognized as territorial, for which both infanticide [29] and cannibalism [30] were reported for males. From a dataset on the simultaneous tracking of individuals with the potential to interact, we can infer about the force of attraction to or repulsion by conspecifics through motion behavior [31].

This study aimed to analyze the determining factors, especially the effect of conspecifics, in space use by jaguars (*P. onca*) in the Pantanal of Brazil. We addressed three groups of questions: (a) Is the movement pattern related to the behavior of maintaining proximity to the home range center? Does this pattern differ between the sexes? (b) Which habitat is selected? Does the selection of habitat vary between the sexes and along the circadian cycle? (c) Is the movement of individuals influenced by the concurrent movement of conspecifics? Are there differences in the individuals' (male or female) movement patterns with respect to intersexual or intrasexual relationships?

We expected that the constraint of movements within proximity to the home range center determined the individuals' space use, and that the selection of habitat varies throughout the circadian cycle due the variations in their circadian cycle activities. We also expected a difference in movement patterns according to sex. Females are inclined to remain near the home range center to optimize the achievement of resources relevant to reproduction and to avert the presence of other conspecifics. In turn, males tend to have a low tolerance to the presence of other males, minimizing antagonistic encounters and presenting a low force of selection towards the home range center, but a high force of selection in relation to the location of females. We believe that our findings can elucidate

the determining mechanisms in space use by animals and, therefore, assist in understanding the biological and ecological needs of such solitary species. This information, combined with landscape management and planning, would make it possible to predict the effects of changes in landscape structure and the effects of the presence or absence of conspecifics on ecological population dynamics.

Material and methods

Study area and habitat characterization

The study was carried out in the Caiman Ecological Refuge, Miranda – MS, Brazil (19°57'02" S, 56°18'14" W) and its surroundings. The property covers an area of 5,600 ha of Private Reserve of Natural Heritage localized within a 53,000 ha farm which encompasses livestock, ecotourism and environmental conservation activities [32]. The area is part of Pantanal biome, its vegetation is characterized by a mosaic of floodable grasslands, Cerrado, semideciduous forest and riparian forest [33]. This biome is influenced by seasonal hydrological cycle [34] and this flood dynamics causes changes in vegetation cover promoting variation from herbaceous to woody formations [33]. Average annual temperatures in the Basis Alto Paraguay vary between 22.5°C and 26.5°C [34] and average annual precipitation is 1,396 mm (ranging from 800 mm to 1,600 mm). The rainy season is from October to April, but the flooded period depends on the declivity of the land and average annual evaporation, which peaks in August [34].

The spatial structure of landscape was represented by a map (Figure III in Supplementary material) classified in ArcGis 10.1 (Environmental Systems Research Institute – ESRI, 2012) and GRASS GIS (Geographic Resources Analysis Support System – GRASS). The land use and cover map was generated using four RapidEye satellite images (2129817 from 24/june/2012; 2129918 from 23/june/2012; 2129818 and 2129917 from 02/07/2012 - provided by CENAP – ICMBio) and one Landsat 5 image (226/074 from 29/september/2011 - obtained from INPE, National Institute for space research - www.inpe.br). We define the mapping area by establishing a 6 km circular buffer around the GPS location points. The distance was defined based on the longest step length recorded in the dataset for the monitored jaguars in a 2h period. The mapping was produced by supervised classification using the maximum likelihood classifier. We edited the polygons

and manually checked the classes by visual inspection on the scale of 1:15,000. Land use and cover classes comprised four categories: water, forest, field/dry pasture, and field/wet pasture.

Jaguar captures and GPS-tracking

Jaguars were captured by the Onçafari Project and the National Center for Research and Conservation of Carnivorous Mammals (CENAP – ICMBio) using a lasso trap. Individuals were anesthetized with intramuscular application of Tiletamine-Zolazepam in an average proportion of 8 mg/kg. After immobilization, collars containing GPS transmitters (Lotek Wireless Fish & Wildlife Monitoring) were attached to nine individuals (three males and six females). The tracking period extended from October 2011 to May 2015. The fixed rate transmission of the locations was not the same for all individuals: seven were located every two hours between the 05:00 and 15:00 and every hour between the 15:00 and 05:00, while two other individuals were located every hour. We obtained 19,910 locations (Table I, Supplementary material) ranging from a minimum of 198 and maximum of 6373 points per individual. An additional camera-trapping monitoring was conducted throughout the period of study with stations distributed unevenly in the Caiman Ecological Refuge, but only camera-trapping information was compiled for the same period for a data acquired simultaneously tracked individuals with collars GPS to verify the presence of other individuals.

Home range estimates and overlapping

Home ranges and the core areas were estimated using the nonparametric Kernel estimator [35] under the isopleth probability of 95% and 50%, respectively. We also estimated the home range and core area that overlapped among individuals, and described the circadian activity pattern calculating the mean of distance moved by individuals by hour. The estimates of home ranges and overlapping areas were carried out using the functions from *adehabitatHR* and *Rgeos* packages available in R software.

Jaguar movements

We used Step Selection Functions (SSF) to evaluate the importance of ranging behavior, habitat type, time of day and distance of conspecifics (males and females) on the jaguars' space use. The SSF is an extension of the widely-used Resource Selection Function (RSF[36]) that incorporates the movement process in the use-availability measurements (see [10]). Firstly, we decompose the whole trajectory of each individual in two components: step length (distance between successive locations) and turning angles (changes of direction between steps). To take into account how resource availability varies across space in according to the current location of the individual, we generated 50 random steps originating from the starting location of each individual step. These set of random steps was generated based on random samples from the observed distributions of step lengths and turning angles. For each endpoint of the observed and random steps, we recorded the habitat type, hour of day, distance to home range center, and the distance to the closest male and female. We used Conditional Logistic Regression (CLR) to fit the SSF (function *coxph* from *Survival* package in R). The CLR was conditioned to each step within each individual (observed steps were scored as "1" while random steps were scored as "0"). We controlled the autocorrelation between successive steps within individual calculating robust standard errors for the coefficients estimated in CLR. The full SSF model for each step i and individual j is described as Selection strength (S) follows the function:

Selectionstrength_{ij}

$$\begin{aligned} = & \beta_1 + \beta_2 \text{Distancefromhomerangecenter}_{ij} * \text{sex}_j + \beta_3 \text{Habitattype}_{ij} \\ & * \text{Timeofday}_{ij} * \text{sex}_j + \beta_4 \text{Distancetomales}_{ij} * \text{sex}_j \\ & + \beta_5 \text{Distancetofemales}_{ij} * \text{sex}_j \end{aligned}$$

We ran eight SSF models, in complexity increasing, to access the support of different competitive models guiding jaguar movement. The models were composed by: ranging behavior (Ran), ranging behavior and its selection with intersexual variation (Ran-sex), habitat (Hab), habitat and its use dependent on the sex (Hab-sex), habitat and its use along the circadian cycle (Hab+Time), habitat and the variation of its selection between

sexes and along the circadian cycle (Hab-sex+Time), conspecific (Con) and conspecific with sexual variation (Con-sex).

We departed from the most basic model, which we assumed that jaguars just move anchored in its home range

$$(Selection\ strength_{ij} = \beta_1 + \beta_2 Distance\ from\ home\ range\ center_{ij}).$$

We included complexity into this basic model by adding sequentially the effects habitat type, habitat type*time of day, distance to males and distance to females. We also permitted sex interacts with habitat type, distance to home range center, distance to males and females because we could expect that habitat selection, ranging behavior and the attraction to males and females can differ between sexes. The conceptual approach used to sequentially add complexity into competitive models is summarized in Table 1. In the first phase, we evaluated the importance of ranging behavior and its sexual differences. The structure of the best ranked model in phase 1 was kept in phase 2. In phase 2, we evaluated the importance of habitat selection and its sexual differences, and kept the best model structure in phase 3. Finally, in phase 3 we evaluated the importance of circadian effects on habitat selection plus the importance of conspecifics on jaguars' movements. We used the Akaike Information Criterion (AIC) [37] for compare the plausibility of the eight competing models. For each model, we calculate the Akaike weights (wAIC) and AIC differences (ΔAIC), which are the relative probability parameters between models and the relative difference between models, respectively.

For all SSF models, we restricted our dataset to only those individuals who were simultaneously tracked and whose home ranges overlapped in some extension. The selection criterion was also restricted to data containing simultaneous locations of females and males. This restriction allows to simultaneously calculate the shortest distance between male-female (M-F), male-male (M-M), female-male (F-M) and female-female (F-F) among individuals with real probability of encountering (overlapped home ranges). All jaguar trajectories sampled every hour were subsampled every two hours to equalize the fix rate among the tracked individuals. Finally, we compiled the camera trap information for the same tracking period to verify the spatio-temporal presence of untracked conspecifics. We recognize individuals from photographic records according to the rosette patterns, while sex was determined from database performed to other studies by CENAP – ICMBio and

Effect of ranging behavior

To access the pure effect of conspecifics on the jaguars' movement, we controlled others more conspicuous effects like habitat type and hour of day. We also incorporated into the model the distance to the home range center (ranging behavior), because individual that have a home range tend to move anchored to the geometric center of its home range (e.g. most home ranges presents circular or elliptical shape). The center of each individuals home range was estimated using Kernel under the isopleth probability of 95%(using the function *gCentroid* from *rgeos* package in R). Values of Selections strength considering only distance from home range center greater than zero indicate that the focal individual selected the distances in relation to its home range center more than the available given the possibilities available at each step. Values equal to zero indicate independent movements to the home range center, and values less than zero when the individual selects less than the available given the possibilities available at each step.

Effect of habitat selection along the time of day

The habitat selection was generated with the support of a map of the study area. The time of day was included in the model using harmonics to allow non-linear effects between selection strength and habitat type [10,40]. Values of Selections strength considering only habitat selection along the time of day greater than zero indicate that the focal individual selected the habitat more than the available given the possibilities available at each step, Values equal to zero indicates independent movements to the habitat and values less than zero indicates avoidance of the habitat when compared with the available habitat. We included four harmonics ($c1_{ij}$, $c2_{ij}$, $s1_{ij}$, $s2_{ij}$) for each step i from individual j :

$$c1_{ij} = \cos\left(\frac{decimal\ hour_{ij} \times 2\pi}{24}\right)$$

$$c2_{ij} = \cos\left(\frac{decimal\ hour_{ij} \times 4\pi}{24}\right)$$

$$s1_{ij} = \sin\left(\frac{decimal\ hour_{ij} \times 2\pi}{24}\right)$$

$$s2_{ij} = \sin\left(\frac{decimal\ hour_{ij} \times 4\pi}{24}\right)$$

Therefore, the interaction term, $\beta_3 Habitat\ type_{ij} * sex * Time\ of\ day$, was modeled as follows:

$$\begin{aligned} &\beta_{3_1} Habitat\ type_{ij} * sex * c1_{ij} + \beta_{3_2} Habitat\ type_{ij} * sex * c2_{ij} + \beta_{3_3} Habitat\ type_{ij} \\ &* sex * s1_{ij} + \beta_{3_4} Habitat\ type_{ij} * sex * s2_{ij} \end{aligned}$$

To verify the existence of a relationship between habitat selection and variations in the cycle of circadian activities, we generated a representation of the activity pattern. The activity patterns of each individual were defined by the average length of the steps taken during the circadian hours. For the species, the activity pattern was defined on the basis of the average of the step lengths of all individuals, and the confidence interval was adjusted by calculating the errors of the averages.

Effect of conspecific

The distance to closest conspecific (male and female) was measured following Delgado et al. [31] approach. We assumed that movement decisions of the focal individual are defined according to the locations of conspecifics at time t_0 , the distance in relation to their conspecifics at time t_1 would represent the decisive responses of attraction or repulsion at time t_0 . Therefore, we measured the observed distance of the focal individual after it has taken a step in its movement (time t_1), as well as the distances of the individual's random steps in relation to the locations of the nearest male and female at time t_0 (Figure 1). Values Selections strength considering only distance to closest conspecific greater than zero indicate that the focal individual was attracted by its nearest neighbor, while values less than zero indicates avoidance of the conspecific.

Results

All individuals were used to estimate the home range and core areas, however, only the five mentioned above were used to carry out the estimations of home range overlap and SSF models. Since we had no simultaneous tracking males in our simultaneous dataset, we

were not able to test the effect of conspecifics male on male's movement (M-M). Five individuals (one male and four females) matched our restriction criteria (individuals tracked simultaneously that presented some extension of home range overlapped), tracked them from October 2013 to January 2014, yielding 17,580 two-hour steps.

During the simultaneous tracking, we recorded four untracked individuals with camera traps within the study area (two adult females, one adult male and another adult which we were not able to determine the sex; Figure 2c). In this period, we also recorded two of the four simultaneous tracked females (F1 and F2) with cubs under their care (Table II, Supplementary material). Three others tracked females (F3, F5, F7) were recorded with small cubs few months before the tracking period. Although, there were not simultaneous records of these females with cubs during the tracking period, we believe there are high probabilities that they were nursing during on that time.

Home range area and overlapping

Home range and core area estimations ranged from 28.87 to 190.12 km² and from 7.42 to 37.73 km², respectively (Table 2). Females tended to present smaller areas than males for both home range (male: mean = 139.28 km² and range = 111.57 to 190.12 km²; female: mean = 77.81 km² and range = 28.87 to 122.86 km²) and core areas (male: mean = 33.66 km² and range = 29.92 to 37.73 km²; female: mean = 19.09 km² and range = 7.41 to 36.56 km²).

The male's home range and core area overlapped just a small extension of the females' areas (0.08 to 0.34 km² for home range and 0 to 0.38 km² for core areas) (Table 3, Figure 3 – items b and c). On the other hand, females presented higher values of overlap among each other (0.07 to 0.72 km²). The highest value (Table 3; F1-F4) occurred among a mother and her independent adult daughter (the relationship was reported for personal communication by researchers of the Onçafari Project based on information provided by visual monitoring the jaguars in study area since 2011).

Jaguar movement

The SSF model ranking suggested the two models that incorporated the movement of conspecifics performed much better than those without it (Table 4), concentrating almost

100% of the supporting evidence (cumulative wAIC ~ 1). These two best models also included the effects of ranging behavior differing between sexes and habitat selection varying through the day.

Effect of ranging behavior

According to the best model (wAIC = 0.79), females presented a strong ranging behavior (tendency to moves anchored to home range center) while the male did not (Figure 2a). Females moved in order to select a maximum distance of 8 km to the home range center, while the male selected greater distances as well as distances farther from the home range center than the available.

Effect of habitat selection along the time of day

Forest and water bodies were selected through the day, mainly at night; however, wet grasslands were avoided in the morning and around midday and used in according its availability mainly at crepuscular period (Figure 2b). The forest presented a larger selection strength compared to other habitats, exhibiting maximum S of 1.3 at 03:00 and minimum of 0 at 19:00. For the water, the maximum S was 0.7 at 04:00 and the minimum was -0.2 at 20:00. For the wet area, the maximum was 0.4 to 16:30 and a minimum of 11.0 at 08:30.

The analysis of the average distance travelled by the jaguars in the Refuge and its surroundings indicates an increase of movement around 15:00 with an average of 0.2 km and decrease around 03:00 with an average of 0.5 km. The largest average distance travelled was 0.7 km at around 19:00 and the smallest were below 0.2 km between 08:00 and 15:00 (Figure 2d).

Effect of conspecific

Male and females moved toward to maximize the chance of encountering with other females (maximum distance of 5 km), but females avoided areas with high likelihood of male encounters, selecting distances greater than 5 km from the male (Figure 2d). The animation showing the spatio-temporal movement dynamics of simultaneously monitored jaguars and an interactive graphic of distances to closest conspecific is represented in Figure II of Supplementary material or can be viewed at: www.leec.eco.br/data/kanda_et al_jaguar_mov.html. In the animation, we observed the meetings between M1 and F2 as well as between F3 and F4.

Discussion

Home range area and overlapping

The core area of activity of male jaguars, considering the standard deviation in the average value of the females' home range, shows to be similar to that found by Cavalcanti and Gese [23] in the Pantanal of southern Brazil (core area: ♂ $34.8 \pm 13.6 \text{ km}^2$ and ♀ $14.5 \pm 6.5 \text{ km}^2$; activity area: ♂ 58.2 to 262.9 km^2 and ♀ 34.1 to 100.8 km^2), although they use radio transmitter and a different estimator with the number of locations ranging from 116 to 1418. In other studies, the areas estimated by the use of radio transmitters varied in males and females according to different numbers of locations and estimators (152.4 km^2 with 84 points for males and 163.25 km^2 with 134 points for females in [22]; and 67.38 km^2 for males and 38.20 km^2 for females with a total of 570 points in [27]). Due to this variation in the methods used to estimate the home range and core area and to the different results in the scientific research [38], inferences of the ecological needs of the species in the Pantanal are still difficult to measure. However, studies correlating the home range and other attributes of the landscape can assist in the understanding of the basic behaviors of animals [17] and the environmental and ecological requirements necessary for the species.

The proportion of overlap between the home ranges and between the core areas associated with the results obtained for sociability and the occurrence of meetings corroborate the evidence that inferences from activity area analyses could indicate the spatial extensions required for the species during the period of monitoring and for the particular landscape. Results of the low overlap of home ranges and core areas of the females with the areas of activities of the male supports the results of sociability, indicating an avoidance behavior of females in relation to the male. Also, the high proportion of overlap between the home ranges of the females (varying from 0.07 to 0.72) indicates an attraction between them in their sociability.

The male overlapped the home ranges of all the females, such that 0.88 of the home range and 0.87 of core area of the female with which there were meetings was situated in his home range. The greatest overlap value between females was of a mother and her independent daughter, which may be some indication of increased tolerance between closely related individuals, as was reported for the maned wolf (*Chrysocyon brachyurus*) [28] and ocelots (*Leopardus pardalis*) [24]. But ecological inferences about the estimate of

home ranges should be cautious since the stability of the area, local loyalties and movement patterns may vary according to seasonality [23] or according to the internal motivations throughout the life of the individual and depending on the spatial scale of analysis [13], showing once again the importance of trying to understand the context of the landscape in which the extent of the home range is formed by each individual.

In the Pantanal, the smallest extensions of home range and the highest density of jaguar individuals [38] may be due to a combination of the abundance and even distribution of food resources [27.42] Thus, other factors could be determining the spatial distribution of the home ranges of the species. Some studies on solitary carnivores suggests that neither the distribution of prey nor the interaction between the distribution of food resources explain the spatial organization [39.43], but the presence of conspecific can determine space use[1].

Jaguar movement

Effect of ranging behavior

Jaguar females move in proximity to the home range center, but the male does not exhibit such behavior. This tendency of females to move preferentially in familiar areas can be related to their reproductive success [16], using experiences gained in previous movements to assist in the location of potential food resources and in maternal care. The male's use of space seems to be determined by the spatial location of females due to the absence of remaining near the home range center and the behavior of maximizing the proximity to females. For small rodents, the determining factor in space use by males was defined by the density and distribution of females [21]. For *Puma concolor*, the quantity and distribution of prey did not explain the spatial organization of male [39].

Effect of habitat selection along the time of day

The jaguar selects different habitats depending on the time of day, and this selection seems to be related to the pattern of circadian activity, with more forest and water selected during their nocturnal activities and wet areas avoided during periods of rest. The selection of different habitats throughout the day has also been reported for wild boar [40] and elk [10] and may be related to different internal motivations in the search for resources for their daily activities [10].

The selection of forest habitats and water appears to be a preference of the species. The use of habitat composed of dense vegetation and associated with the water appears to be a tendency for the species in Brazil [38], and despite the Pantanal consisting of humid environments, the jaguars were rarely found far from permanent water bodies [22]. The distinction in selecting these habitats can be related to a preference for consuming wild prey associated with forest environments and water, such as caimans, peccaries, capybaras, tapirs, wild boar and marsh deer [30, 38.41].

Effect of conspecific

P. onca male and females both move to maximize their proximity to females, while females avoided the male. Despite the report by Cavalcanti and Gese [23] of the absence of influence of conspecifics on the movement of jaguar in the Pantanal, the high proximity between their conspecifics (< 200 m) indicates some degree of tolerance in space use. This flexibility has also been described in other solitary carnivores, with a lack of use of exclusive areas [15,22-24,27] and a strong intersexual spatial association between pairs of individuals (distance \leq 200 m and time \leq 4 hours [25]; distance \leq 100 m and time \leq 1 hour [26]). These results corroborate the assumptions that in solitary carnivores the decrease in direct interference interactions between conspecifics can occur in other dimensions in the ecological niche and not the spatial dimension, where they would restrict the use of individual spatial regions known as territories.

Although F2 had cubs under its care, this female had encounters with the male. This sighting has been reported in the literature on jaguars in the Pantanal [23], but it is not yet known which mechanisms occur to prevent infanticide, as was reported by Soares et al. [29]. The estimations of the dates of birth of the cubs in this study and in that of Cavalcanti and Gese [23] indicate a lack of an established period for reproduction, so the females would be receptive at different times throughout the year. This information together with the evidence of cognitive ability and spatial memory in mammals [14.17 -19] could aid in the ecological understanding of the species and the investigation of whether males use specific areas to enhance the locations of receptive females throughout the year.

Our study brings new light on the understanding of how the presence of conspecifics can influence patterns of movements and, thus, determine space use by the animals. This is particularly important because allow us better understand which are the

main mechanisms that govern space use by animals, and as consequence provide more in deep information about the biological and ecological needs for the conservation of the species worldwide. At the same time, our findings reinforce the influence of landscape structure and dynamic on the fauna populations, in especial those that can be influenced by the presence or absence of conspecifics.

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Table 1- Conceptual approach to sequentially generate the competitive models in increasing of complexity in the analysis of resource selection. The prevalence of each variable composing the best models was followed according to the Akaike Information Criteria (AIC).

Phase 1 - Models	Phase 2 - Models	Phase 3 - Models
Selection ~ Ranging behavior	Selection ~ Phase1	Selection ~ Phase 2
Selection ~ Ranging behavior *Sex	Selection ~ Phase1+Habitat	Selection ~ Phase2*Time
	Selection ~	Selection ~ Phase2*Time +
	Phase1+Habitat*Sex	Conspecifics
		Selection ~ Phase2*Time +
		Conspecifics*Sex

Table 2-Home range (Kernel 95%) and core area (Kernel 50%) estimates (in km²) for nine jaguar individuals tracked in the Caiman Ecological Refuge – MS, Brazil and its surroundings. ID=jaguar identity, M = Male, F = Female.

ID	Sex	Kernel 50%	Kernel 95%
M1	M	37.73	190.12
M2	M	29.92	116.16
M3	M	33.33	111.57
F1	F	15.48	76.10
F2	F	13.64	75.76
F3	F	36.56	122.86
F4	F	28.59	111.76
F5	F	12.85	51.57
F6	F	7.42	28.87

Table 3—Home-range (Kernel 95%) and core area (Kernel 50%) overlapping (%) among five jaguars simultaneously tracked in the Caiman Ecological Refuge – MS, Brazil. M = Male, F = Female. Values in the columns represent the proportion of the area occupied by individuals presented in the lines. ID=jaguar identity, M=Male, F=Female.

ID	M1	F1	F2	F3	F4
M1	1	0.14 (0.09)	0.34 (0.38)	0.12 (0)	0.08 (0.03)
F1	0.38 (0.18)	1	0.28 (0.04)	0.71 (0.54)	0.72 (0.64)
F2	0.88 (0.87)	0.27 (0.04)	1	0.11 (0)	0.16 (0)
F3	0.19 (0)	0.44 (0.23)	0.07 (0)	1	0.48 (0.16)
F4	0.14 (0.03)	0.49 (0.36)	0.11 (0)	0.53 (0.21)	1

Table 4—Model ranking of the eight competitive SSF models generated from data of the simultaneous monitoring of five jaguars in the Caiman Ecological Refuge and its surroundings, Miranda – MS, Brazil, based on the Akaike Information Criterion (AIC). k=number of parameters; wAIC=weight of the models; Δ AIC =difference between the largest AIC value and the lowest AIC value. Ranging behavior (Ran), Ranging behavior and the intersexual variation of its selection (Ran-sex), habitat (Hab), habitat and its use along the circadian cycle (Hab+time), conspecific (Con) and conspecific with sexual variation (Con-sex).

Models	LogLikelihood	k	AIC	wAIC	ΔAIC
Ran-sex+Hab+Time+Con	-37092.51	19	74223.03	0.71	0
Ran-sex+Hab+Time+Con-sex	-37091.39	21	74224.79	0.29	1.76
Ran-sex+Habitat+Time	-43396.33	17	86826.67	0	12603.64
Ran-sex+ Hab	-43498.09	5	87006.17	0	12783.15
Ran-sex+Hab-sex	-43495.44	8	87006.89	0	12783.86
Ran-sex	-43585.94	2	87175.88	0	12952.86
Ran	-43586.98	1	87175.95	0	12952.93
Null	-43647.7	1	87297.4	0	13074.37

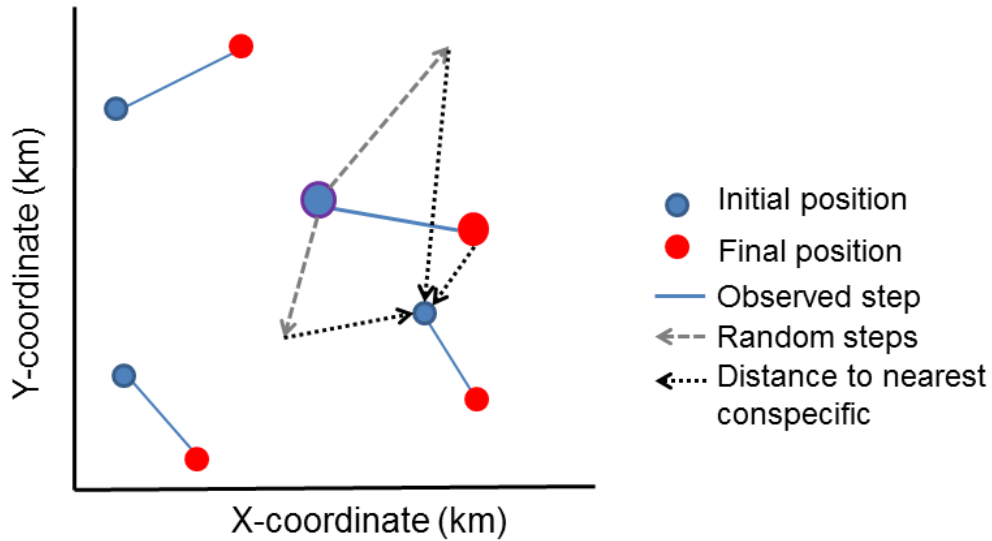


Figure1- Schema showing how we calculated the distance to conspecifics step by step. Large circles depict the focal individual and small circles depict the conspecifics (in this example, three individuals) moving in the landscape. Blue circles indicate the starting location (time t_0) and red circles indicate the final location of the individual (time t_2). Solid blue lines represent the steps taken, gray dashed arrows indicate random steps of the focal individual, and dotted black arrows indicate the measured distances of steps taken and the random steps of the focal individual. Adapted from Delgado et al. [31].

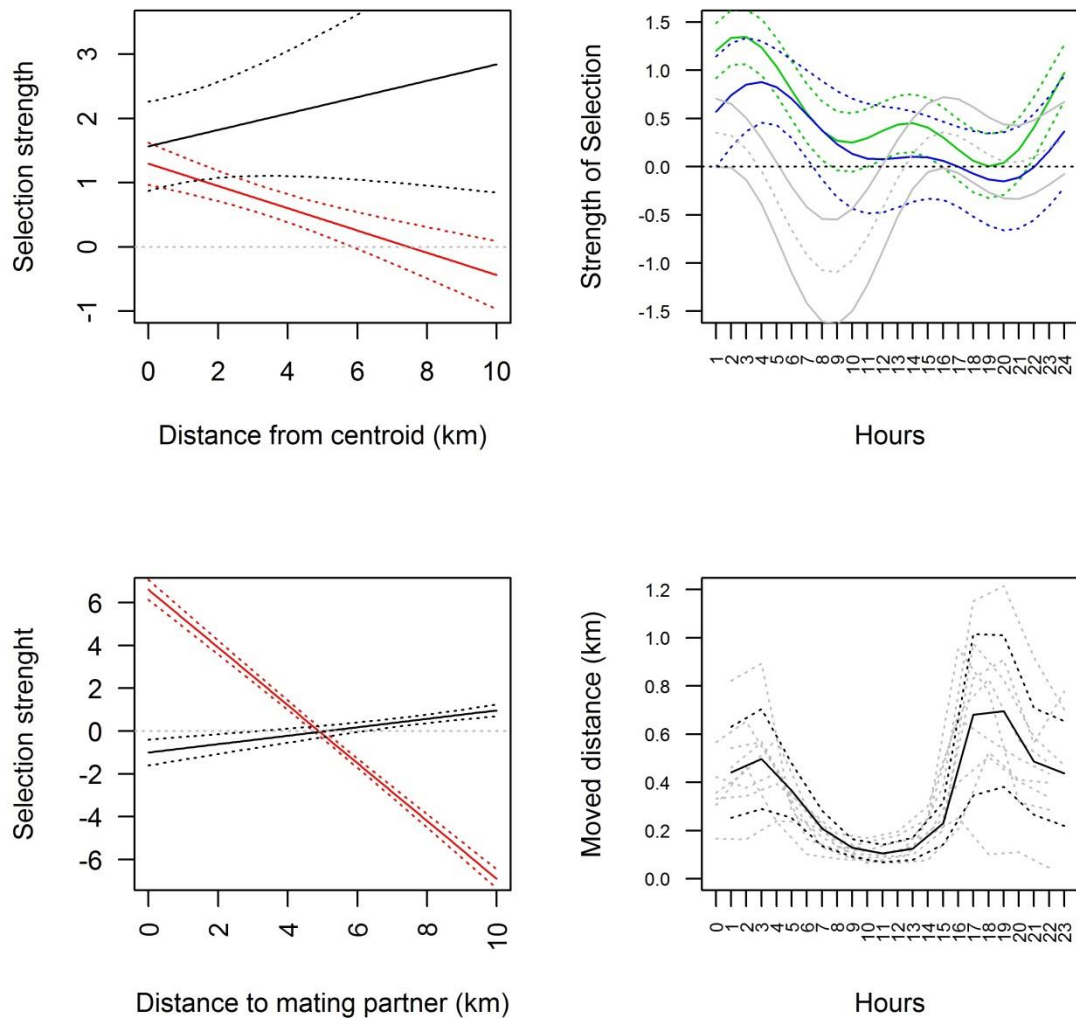


Figure 2—Circadian activity patterns as well as the ranging behaviour, habitat selection and conspecifics effects on jaguars' movement (based on the best ranked model; Table 2) (a) Selection strength in relation to the distance to the nearest conspecific. Red line indicates the effect between females (F-F) and between a male and females (M-F). Black line represents the close relationship between a female and a male (F-M). (b) Habitat selection strength through the hours of the day. Forest, water bodies and wet grasslands are represented by green, blue and gray colors, respectively. (c) Selection strength in relation to distance from the home range center for males (black) and females (red). For all panels, solid lines represent the estimated selection strength while dashed lines around them depicts the 95% confidence interval of the estimates. Dotted lines around the solid lines represent

the 95% confidence interval.(d) In black, the mean of distance moved (km) through the day. Each dashed gray line depicts one observed individual.

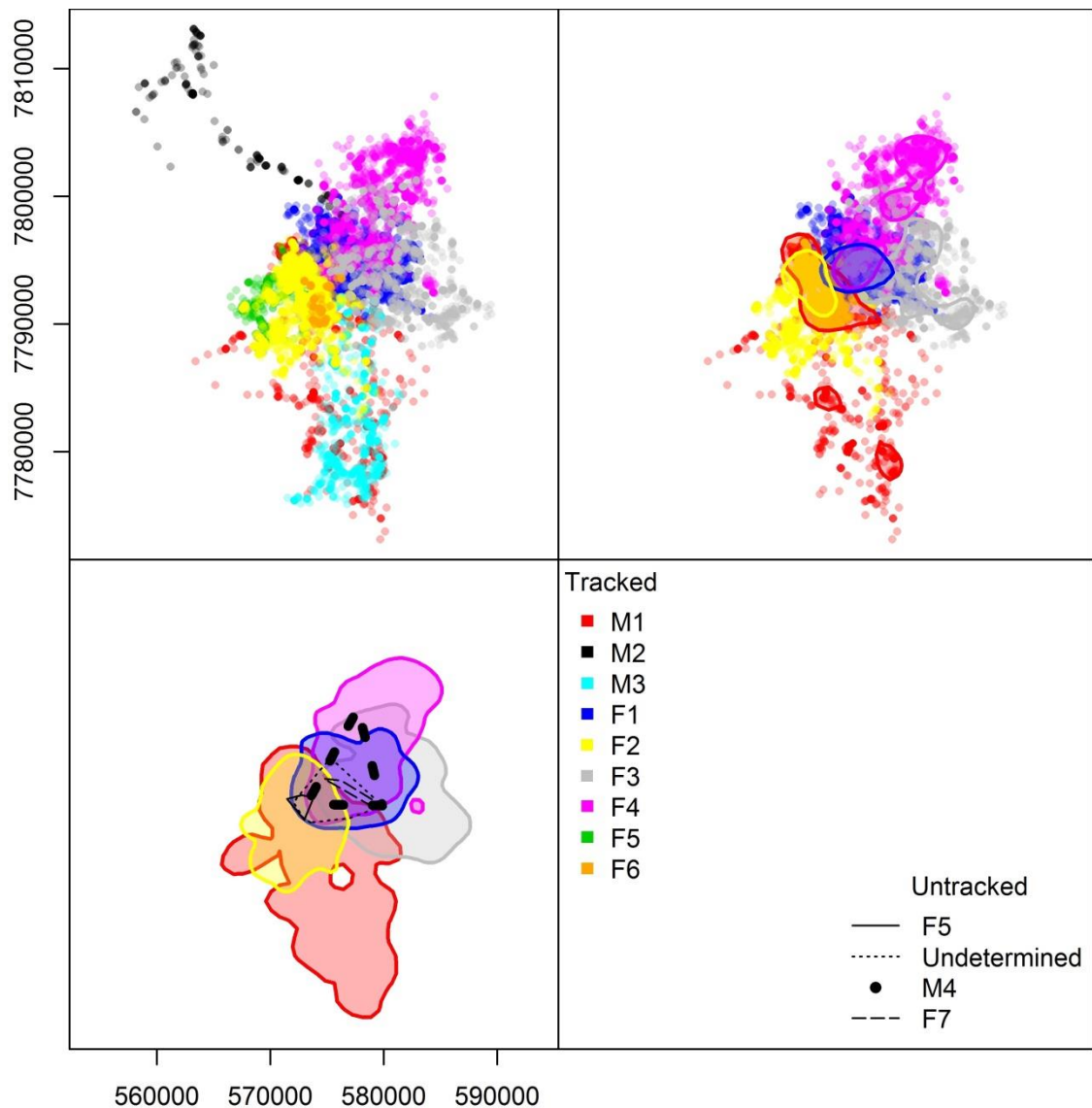


Figure 3-Spatial locations of individuals monitored by GPS collars and cameras. (a) Distribution of tracking time in Julian days of nine *P. onca* individuals located in the Caiman Ecological Refuge and its surroundings, Miranda – MS. Different colors in each row represent the distribution of data obtained for every Jaguar. M1=red dots; M2=black dots; M3=cyan dots; F1=blue dots; F2=yellow dots; F3=gray dots; F4=pink dots; F5=green dots; F6=orange dots. Lines represent core areas of each individual. (b) Spatial Locations of a male (M1) and four females (F1, F2, F3, F4) monitored simultaneously and their core areas in the Caiman Ecological Refuge and its surroundings, Miranda – MS. (c) Locations of the home ranges of five individuals simultaneously monitored with GPS collars and the locations of other individuals recorded in the same monitoring period by camera traps.

Supplementary material

Information on the monitoring of nine *P. onca* individuals

The exclusion of monitoring information due to problems in data transmission was a loss of 2,200 locations (16.25%) of the total 13,539 locations for eight Jaguars. A maximum difference of four minutes between the hours of locations of the individuals accrued during the standardization of the interval of the data to every two hours.

Table I - Information of the monitoring of the jaguar in the Caiman Ecological Refuge and its surroundings, in the Pantanal of southern Brazil. ID=jaguar identity, M=Male, F=Female.

ID	Sex	Monitoring Period	Data transmission	Total locations
M1	M	Oct. 2013 to Jan. 2014	05:00-15:00, every 2 hours 15:00-05:00, every hour	1340
M2	M	Apr 2012 to Apr. 2012	05:00-15:00, every 2 hours 15:00-05:00, every hour	198
M3	M	Nov. 2011 to Dec. 2011	Every hour	1065
F1	F	Oct. 2012 to Nov. 2013	05:00-15:00, every 2 hours 15:00-05:00, every hour	6373
F2	F	Apr 2013 to Jan. 2014	05:00-15:00, every 2 hours 15:00-05:00, every hour	4931
F3	F	Oct. 2013 to Jan 2014	05:00-15:00, every 2 hours 15:00-05:00, every hour	1421
F4	F	Oct. 2013 to May 2014	05:00-15:00, every 2 hours 15:00-05:00, every hour	3519
F5	F	Oct. 2011 to Jan. 2012	Every hour	852
F6	F	Jun. 2012 to Jun. 2012	05:00-15:00, every 2 hours 17:00-05:00, every hour	211

Information on camera traps

The camera traps' information was compiled for the same period as the data chosen for the resource selection analysis, obtained between 10/21/2013 and 12/27/2013. The twenty-three stations were distributed unevenly in the landscape, occupying around 27.37 km² (3%) of 913.04 km² within the boundary of the 6 km distance established for the data on five of the simultaneously monitored jaguars (Figure II). The sampling effort was different at every station, ranging from 24 to 2760 hours.

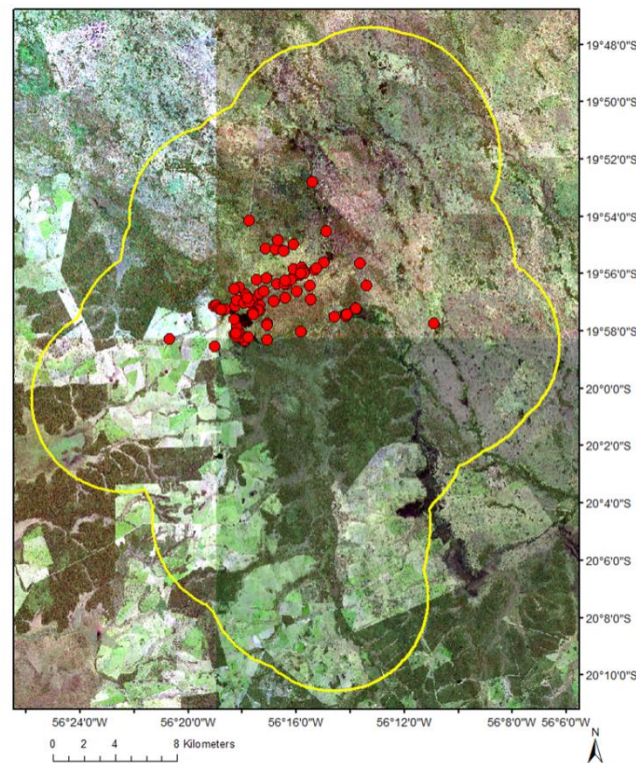


Figure II-locations of twenty-three camera trap stations in the Caiman Ecological Refuge, Miranda – MS. Yellow boundary represents the distance of 6 km between simultaneous monitoring points of five jaguars.

Table II –Information of the last record of females with cubs during monitoring with camera traps in the Caiman Ecological Refuge, Miranda – MS.

Individual	Date of the last record	Number of cubs	Approximate age of cub
F1	07/01/2014	1	8 months
F2	16/01/2014	1	8 months
F3	12/08/2013	1	undetermined
F5	27/06/2013	1	17 months
F7	15/05/2013	1	9 months

Landscape mapping details

The landscape dimension was 1317.25 km² and its composition was 634.56 km² (48.17%) field/wet pasture, 394.03 km² (29.91%) of forest, 280.12 km² (21.26%) field/dry pasture and 8.54 km² (0.65%) of water (Figure III).

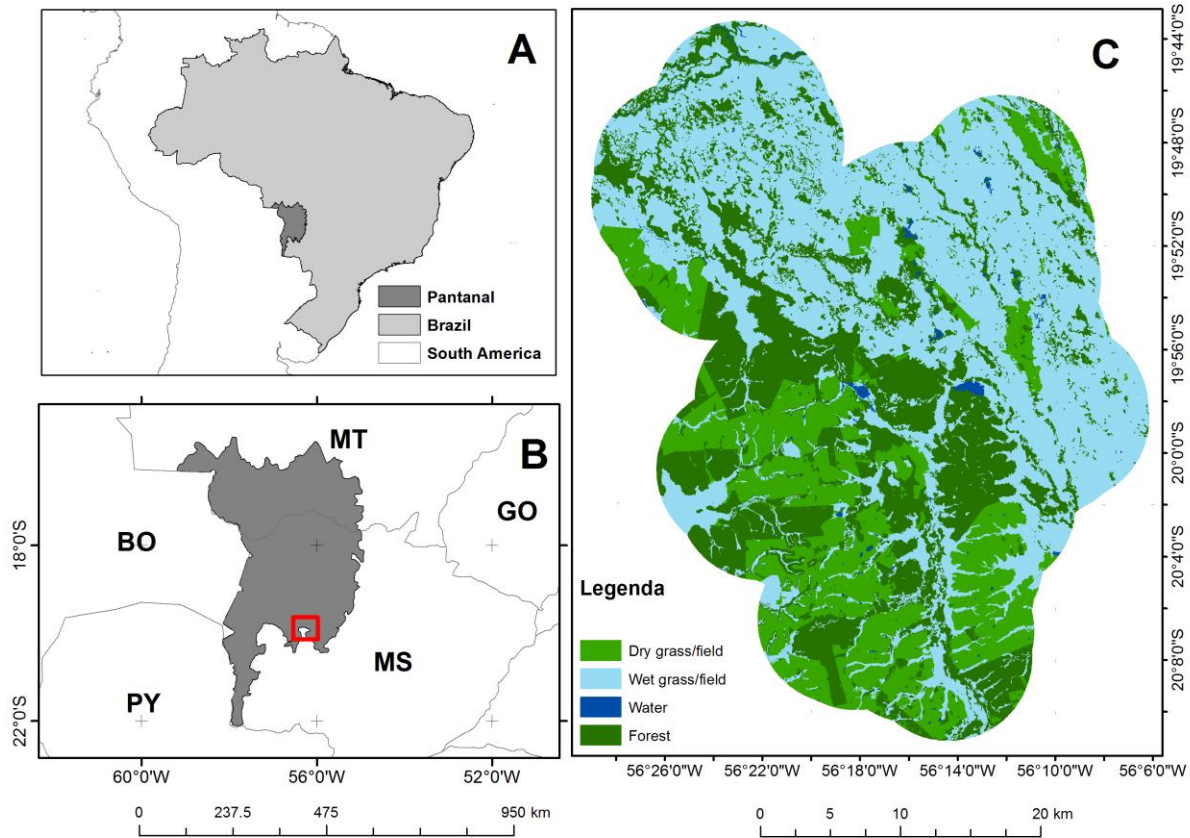


Figure III-A) Location of the Pantanal Biome in Brazil. **B)** Location of the Caiman Ecological Refuge, Miranda – MS in the Pantanal, southern Brazil. MT=Mato Grosso; GO=Goiás; MS=Mato Grosso do Sul; BO=Bolivia; PY=Paraguay. **C)** Map of the area where nine jaguars were monitored.

Animation showing the dynamics of spatio-temporal movement between simultaneously monitored *Panthera onca* individuals

The animation was composed of two interactive scenarios: one scenario reproduced the movement dynamics of the individuals simultaneously monitored with GPS collars in space and time, while the other depicted the distances between the male and the nearest female and between the most proximate females shown in the first interactive scene.

The landscape of the monitoring location of the individuals in the first scenario was obtained by satellite imagery from Google Earth. The colored polygons represent the home range of each individual by the 95% fixed Kernel; the colored dots are the individual locations; and the colored lines are the distances in km between the male and the nearest female (MF) and between the most proximate females (FF). Events of encounters between these pairs are marked on the map with small black dots. Data external to the scenarios indicate the year, month, day, and the hours (local time) of the location data, synchronized with the reproductions presented in the image.

The second scenario of the animation represents the distances in km between the male and the nearest female (black continuous line) and between the most proximate females (continuous red line), synchronized with the reproductions of the spatio-temporal dynamics presented in the first scene. In the scenario, the vertical axis indicates the distance and the horizontal axes indicates the Julian days. Throughout the animation, the gray vertical lines indicate the encounter events of the relationships between the individuals.

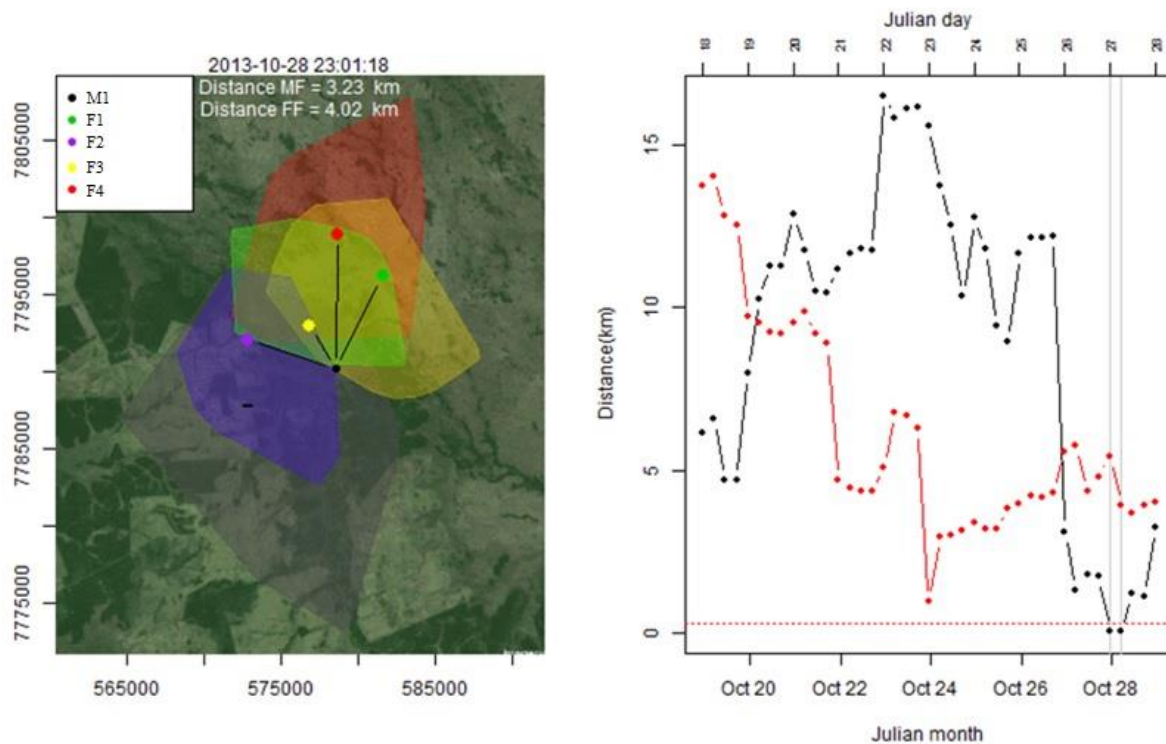


Figure IV-Illustration of the animation of the movements made by five *P. onca* individuals monitored simultaneously in the Caiman Ecological Refuge and its surroundings, Miranda – MS. Obtained from the satellite image from Google Earth. The animation can be viewed at: www.leec.eco.br/data/kanda_etal_jaguar_mov.html

4. Conclusões gerais

A onça-pintada (*P. onca*) mostra possuir uma preferência pela seleção de habitats florestal e água e esta seleção parece estar relacionada com o padrão de atividade circadiana, selecionando mais florestas e água durante as suas atividades de caça noturnas e, evitando áreas úmidas nos períodos de seu descanso. Desta forma, a perda e fragmentação de habitats florestais na área de ocorrência da espécie podem ser consideradas ameaças à conservação desta espécie em risco de extinção.

Os padrões de uso do espaço de um organismo são influenciados por três componentes principais: o comportamento em permanecer próximo ao centro de sua área de vida, a seleção do habitat com variação ao longo do ciclo circadiano e pelo movimento dos coespecíficos. O grau de seleção de cada componente pode variar de acordo com o gênero sexual.

Assim, além da perda e fragmentação de habitats florestais em toda ocorrência da onça-pintada, a caça mostra-se ser mais um fator preocupante para a conservação desta espécie, já que o uso do espaço é determinado pela presença de seus coespecíficos e a exclusão ou inclusão de um indivíduo pode afetar toda a dinâmica ecológica populacional desta espécie.

Nossos resultados contribuem para o entendimento dos mecanismos comportamentais subjacentes no uso do espaço durante o processo de movimento e como os animais movem-se na presença dos coespecíficos. Essa compreensão poderá auxiliar nas possíveis previsões dos efeitos das variações na estrutura da paisagem para a conservação dessa espécie.