# Illuminating Big Cat Movements: Does Moonlight Influence Jaguar Space Use in the Southern Pantanal?

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**ABSTRACT –** In light of increasing levels of habitat loss and modification, knowledge on the environmental factors that influence space use by large carnivores emerges as crucial for effective conservation efforts. Despite a growing body of literature exploring moonlight influence on the activity of felid apex predators, its effects on jaguars (*Panthera onca*) remain largely understudied - including in the Brazilian Pantanal. This wetland is currently undergoing significant human-driven changes with the expansion of agricultural activities, and retaliatory killing of jaguars arises as one of the main threats to the species' persistence. Here we studied the influence of variation in nocturnal luminosity on jaguars' space use in the southern Pantanal. We analyzed GPS data of collared jaguars in fields potentially used as pastures considering the distance to the closest forest and luminosity in the context of low, medium and high moonlight intensities. We found that although jaguars tend to remain close to forest surroundings throughout the lunar cycle, they venture deeper in pastures under medium to high moonlight illumination. We suggest that jaguars' pasture use at our study site fits the predation risk hypothesis, where species at higher trophic levels tend to be more active with moonlight as it allows for greater predation success – especially considering that forest edges can provide shelter and facilitate stalking of cattle. Although we did not focus on predation success in our analysis, we recommend herds to be kept away from forest edges and the placement of physical barriers (e.g. fences) to prevent opportunistic jaguar attacks – especially on brighter nights.

**Keywords:** Wetlands; human-wildlife conflict; social-ecological systems.

## O Uso do Espaço pela Onça-Pintada é Influenciado pela Luz da Lua? Iluminando o Movimento de Felinos de Grande Porte no Sul do Pantanal

**RESUMO –** Diante dos níveis crescentes de perda e modificação de habitat, conhecer os fatores ambientais que influenciam o uso do espaço por grandes carnívoros é crucial para esforços de conservação efetivos. Apesar da crescente literatura investigando o efeito da luminosidade da lua sobre felídeos topo de cadeia, tais efeitos sobre a onça-pintada (*Panthera onca*) ainda precisam ser explorados – inclusive no Pantanal brasileiro. O bioma passa, atualmente, por alterações humanas significativas diante da expansão da prática agropecuária, e a caça por retaliação se caracteriza como uma das principais ameaças à persistência das onças no Pantanal. Estudamos a influência da variação da luminosidade noturna no uso do espaço pela onça-pintada no Pantanal Sul. Analisamos dados de localização GPS obtidos via monitoramento de onças com rádio-colares em campos potencialmente utilizados como pastagens, considerando a distância da floresta mais próxima e a luminosidade em cenários de baixa, média e alta intensidade luminosa da lua. Observamos que, embora as onças permaneçam nas imediações das florestas ao longo do ciclo lunar, elas adentram mais as pastagens sob média a alta luminosidade da lua. Sugerimos que o uso do espaço pela espécie na área de estudo investigada sustenta a 'hipótese de risco de predação' (predation risk hypothesis), onde espécies que ocupam níveis tróficos mais altos tendem a ser mais ativas sob luminosidade noturna, já que esta possibilita maior sucesso de predação – especialmente considerando que bordas de floresta podem servir como abrigo e favorecer a emboscada do gado.


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Apesar de não termos focado em sucesso de predação na nossa análise, recomendamos que rebanhos sejam mantidos afastados de bordas de floresta, bem como que sejam implementadas barreiras físicas (ex. cercas) para prevenção de ataques oportunistas das onças aos animais de criação – particularmente em noites mais claras.

**Palavras-chave:** Áreas úmidas; conflito homem-animal; sistemas socioecológicos.

## Iluminando el Movimiento de Grandes Felinos en el Sur del Pantanal: ¿Influye la Luz de la Luna en el uso del Espacio por Parte del Jaguar?

**RESUMEN –** Debido a los crecientes niveles de pérdida y modificación del hábitat, el conocimiento de los factores ambientales que influyen en el uso del espacio de los grandes carnívoros resulta crucial para esfuerzos de conservación efectivos. A pesar de un creciente cuerpo de literatura que explora la influencia de la luz de la luna en la actividad de los depredadores ápice félidos, sus efectos sobre los jaguares (*Panthera onca*) siguen siendo en gran parte poco estudiados - incluso en el Pantanal brasileño. Este bioma está experimentando cambios significativos impulsados por el ser humano con la expansión de las actividades agrícolas, y la matanza de jaguares como represalia surge como una de las principales amenazas para la persistencia de la especie. Estudiamos la influencia de la variación en la luminosidad nocturna en el uso del espacio de los jaguares en el sur del Pantanal. Analizamos datos de GPS de jaguares con collar en campos potencialmente utilizados como pasturas considerando la distancia al bosque más cercano y la luminosidad en contextos de luz de luna de baja, media y alta intensidad. Descubrimos que, aunque los jaguares tienden a permanecer cerca de los alrededores del bosque durante todo el ciclo lunar, se aventuran más profundamente en los pastizales bajo una luz de luna media a alta. Sugerimos que el uso de pastos de jaguares en nuestro sitio de estudio se ajuste a la hipótesis del riesgo de depredación (predation risk hypothesis), donde las especies en niveles tróficos más altos tienden a ser más activas con la luz de la luna, ya que permite un mayor éxito de depredación, especialmente considerando que los bordes del bosque pueden proporcionar refugio y facilitar el acecho al ganado. Aunque en nuestro análisis no nos enfocamos en el éxito de la depredación, recomendamos que los rebaños se mantengan alejados de los bordes del bosque y la colocación de barreras físicas (e.j. cercas) para prevenir ataques oportunistas de jaguares, especialmente en las noches más brillantes.

**Palabras clave:** Humedales; conflicto hombre-vida silvestre; sistemas socio-ecológicos.

## Introduction

There are growing concerns about the detrimental consequences of the ongoing human-driven defaunation processes affecting ecosystem functioning and human well-being (Dirzo *et al.*, 2014; Young *et al.*, 2016). The dominant drivers of defaunation in terrestrial environments consist of habitat loss and modification, where South America emerges as one of the main global hotspots of extinction risk for terrestrial vertebrates (Young *et al.*, 2016). In this context, larger animals are especially affected, thus the need to model top predators' habitats and better understand their environmental requirements – particularly in landscapes under land-use transformation pressure (Dirzo *et al.*, 2014; Zeilhofer *et al.*, 2014; Young *et al.*, 2016; Morato *et al.*, 2018).

Amidst the expansion of human-altered landscapes, wetlands stand out as one of the most affected ecosystems (Díaz *et al.*, 2019). Over 85% of wetlands have been lost globally mainly due to agricultural and urban growth (Díaz *et al.*, 2019). Concerning the Brazilian wetlands in the Pantanal region, Miranda *et al.* (2018) predict that in 2030 this important system will have over 3/4 of its area covered by short vegetation. The authors further suggest that only 14% of the Pantanal area will be covered by dense vegetation (such as forests) by then as low-impact traditional practices – such as cattle ranching – are progressively replaced with high-impact models of production. This is likely to affect and alter the entire system dynamics, particularly flood pulse (Miranda *et al.*, 2018), also exerting even greater pressure on the survival of one of its most iconic mammals – the jaguar (*Panthera onca*).

Large carnivores like jaguars are fundamental for structuring trophic communities and for the maintenance of ecosystems (Ripple *et al.*, 2014). Jaguars are the biggest wildcats of the Americas, occurring in approximately 47% of the Pantanal (Morato *et al.*, 2013). Conflicts involving the presence of jaguars and cattle farming activities arise as the result of livestock depredation, which ultimately leads to retaliatory killing of this top predator – one of the greatest threats to the species in the Brazilian Pantanal (Morato *et al.*, 2013; Balbuena-Serrano *et al.*, 2020; Romero-Muñoz *et al.*, 2020) where the jaguar is categorized as Vulnerable to extinction risk (Morato *et al.*, 2013). The species' peak activities tend to occur at dawn and dusk with low activities during daytime in this system (Cavalcanti & Gese, 2009; Kanda *et al.*, 2019). Furthermore, recent research highlights the importance of forest habitats and water bodies for jaguars (Zeilhofer *et al.*, 2014; Morato *et al.*, 2016; Morato *et al.*, 2018; Kanda *et al.*, 2019).

Seminal studies exploring jaguars' ecology in the Pantanal, including movement and activity patterns, habitat use, and jaguar-cattle conflicts, date back to the 1980s and 1990s (e.g. Schaller & Crawshaw, 1980; Crawshaw & Quigley, 1991; Quigley & Crawshaw, 1992). Nearly 40 years later, Balbuena-Serrano *et al.* (2020) identified a small percentage of areas under high livestock depredation risk in the Pantanal region (around 7%) in terms of jaguars' attacks. They describe important environmental factors that characterize depredation hotspots (e.g. proximity to livestock herding areas where peripheral vegetation functions as shelter and stalking facilitator).

Knowledge on landscape characteristics and other external environmental factors that influence the access of predators to prey is fundamental for proper livestock management by farmers in order to prevent losses (Miller *et al.*, 2015; Robertson *et al.*, 2019). It also can ultimately lead to the avoidance of retaliatory killing of opportunistic predators like jaguars (Tortato *et al.*, 2015). However, the effect of moonlight variation on jaguars' activity, behavior, predation, habitat selection and use as well as movement patterns in the Pantanal remains largely understudied. This study attempts at taking the initial steps towards filling this research gap.

In light of highly variable species' responses to moonlight (Prugh & Golden, 2014), studies focusing on felid apex predators illustrate the distinct reactions that these carnivores show to the lunar cycle. Regarding lions (*Panthera leo)*, while their predation success has been reported as greater on darker nights with significantly more events of livestock depredation coinciding with lower moonlight levels (Packer *et al.*, 2011; Preston *et al.*, 2019; Robertson *et al.*, 2019), the (lack of) influence of moonlight variation on their movement patterns present researchers with a puzzling topic. Cozzi *et al.* (2012) and Preston *et al.* (2019), for example, found no moonlight influence on lions' movements. But Oriol-Cotterill *et al.* (2015) observed that this species transits closer to livestock enclosures with decreasing moonlight. As for cougars (*Puma concolor*), the species does not seem to be affected by moonlight variation (Harmsen *et al.*, 2011; Soria-Díaz *et al.*, 2016; Pratas-Santiago *et al.*, 2017; de Matos Dias *et al.*, 2018). Finally, the influence of the lunar cycle on jaguars' main prey species is suggested as indirectly affecting jaguar activity (Harmsen *et al.*, 2011; Montalvo *et al.*, 2020). Harmsen *et al.* (2011) observed that armadillos in Belize reduced their activity during periods of brighter illumination and so did jaguars in locations where armadillos were important prey for them. Montalvo *et al.* (2020) noted that jaguars' activities in Costa Rica interact with sea turtle nesting peaks, which in turn are influenced by moonlight variation. Sea turtles constitute an important resource for jaguars in this location - especially females with offspring (Montalvo *et al.*, 2020).

Here we take the initial steps in exploring the extent to which the interplay between landscape features and moonlight variation influences jaguars' movements in the Pantanal. Our objective was to better understand the species' space use in non-forest areas. We focus on GPS location points of collared jaguars in areas potentially used as pastures considering the distance to the closest forest and luminosity – i.e. the average proportion of the moon's surface illuminated on specific nights (e.g. Packer *et al.*, 2011). Although not our focus, we acknowledge that predation dynamics is an important component when assessing moonlight influence on the movement ecology of top predators (e.g. Prugh & Golden, 2014; Pratas-Santiago *et al.*, 2017). We expected to find that the depth gradients of jaguars' location points indicate selection for areas closest to forests throughout the lunar cycle, with more pronounced evidence of the selection for forest surroundings under high moonlight intensity given jaguars' inconspicuous behavior. Our main goal is that consideration of the lunar cycle and landscape features allow for enhanced insights on jaguar ecology and conservation as it connects with cattle management, thus contributing to addressing the threats to which the species is increasingly exposed – particularly habitat loss and modification, and retaliatory killing.

## Material and Methods

### Study area

The study area (figure 1) consists of the Caiman Ecological Refuge (19°57'39"S/56°18'20"O) and its surroundings. The Refuge occupies an area of approximately 53,000 ha within the Pantanal region and roughly 5,603 hectares are protected as a private natural heritage reserve (RPPN under the Brazilian environmental law). The enterprise combines cattle farming, ecotourism and environmental conservation activities since 1980 (Refúgio Ecológico Caiman, 2016). The study area totals ~131,000 ha of which 91,400 ha, or ~69.8%, correspond to fields; 39,400 ha, or ~30%, are forests; and, finally, water bodies correspond to less than 1 thousand ha. Large areas of land are devoted to cattle farming in the Pantanal and livestock is almost exclusively kept free in the farms, on native pastures, except in protected areas (Abreu *et al.*, 2010; Araujo *et al.*, 2018). Thus, all fields are assumed potential pastures in our study.

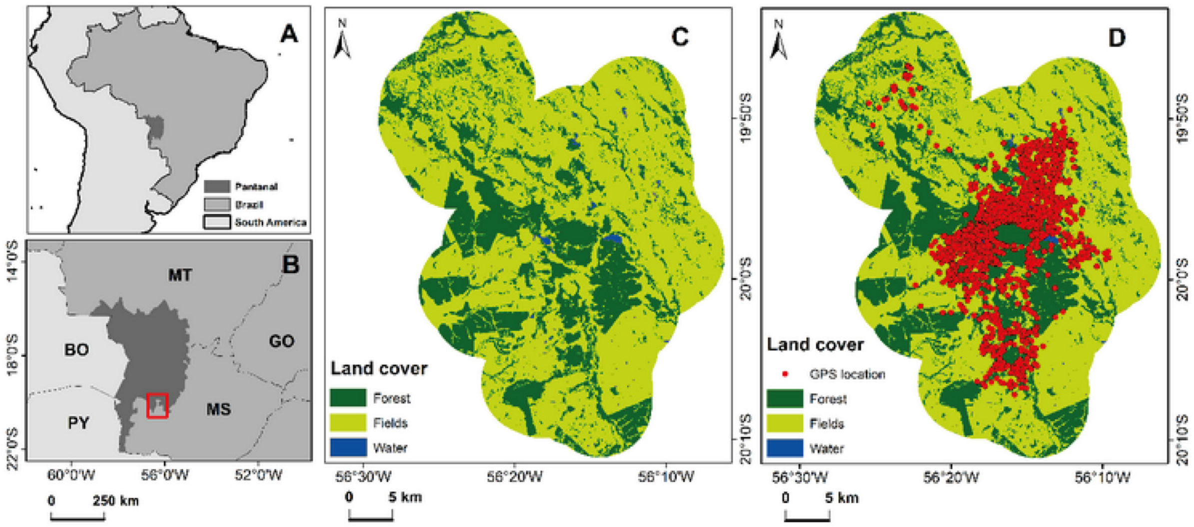


Figure 1 – Study area at the Caiman Ecological Refuge and surroundings, located in Miranda – MS, Brazil. A) Pantanal region (dark gray) within the Brazilian territory (medium gray); B) Red rectangle indicating our study site in the Pantanal region, Brazil; C) Map of land cover classification of the study area. Area depicted originating from a 6km buffer based on all GPS location points of collared jaguars. The total area analyzed consists of forest areas (dark green), fields/pastures (light green) and water bodies (blue); D) Red dots represent the GPS location points of the monitored jaguars that were considered for analysis. Further details regarding map elaboration are available in the supplementary material.

### Jaguars' monitoring

Jaguars were captured by the Onçafari Project (https://oncafari.org/en/) in collaboration with the Brazilian National Research Center for Carnivores Conservation – CENAP (https://www.icmbio.gov.br/cenap/) using soft-hold foot-snare traps (de Araujo *et al.*, 2021; Frank *et al.*, 2003). They were anesthetized with an intramuscular application of Tiletamine-Zolazepam on an average proportion of 8 mg/kg (Morato *et al.*, 2001). Following immobilization, the GPS collars – Lotek Wireless Fish & Wildlife Monitoring – were placed on nine jaguars, three males and six females. The capture protocol was approved by the Chico Mendes Institute for Biodiversity Conservation – ICMBio (Licence SISBio/ICMBio n° 30053).

The monitoring period occurred from October 2011 to May 2014, and data collection intervals differed among the monitored individuals. This led us to consider all monitoring data together as opposed to performing individual or sex-specific analyses. The fixed transmission rate of locations varied among jaguars: seven every two hours between 5 am and 3 pm and every hour between 3 pm and 5 am; the other two monitored individuals had their location points registered every hour (see jaguars' IDs, monitoring period, transmission scheme, total of location points registered per individual and total of location points considered for analysis per individual in supplementary material). To reduce location errors the data was previously filtered and all fixes with dilution of precision > 5 am were excluded (Bjorneraas *et al.*, 2010).

## Moonlight information and selection of jaguars' location data

Moon transit differs in each moon phase, hence the variation in moon brightness between different phases and times of the night (Pratas-Santiago *et al.*, 2017). Therefore, we created a nighttime-specific subset of location data that only included location points when the moon was visible at our study site (-4 hours Greenwich Mean Time) based on moonrise, moonset, sunrise and sunset information from the R package suncalc (Milone *et al.*, 2018; Thieurmel & Elmarhraoui, 2019). We also used moonrise, moonset, sunrise and sunset information for the day before and the day after the GPS location data when the time registered for a given location point was close to the transition from one day to the next. We thus arrived at 12,606 location points registered at night and when the moon was visible in our study area (out of 19,909 location points obtained via GPS tracking of the nine jaguars monitored).

The illuminated fraction of the moon, as described by Thieurmel & Elmarhraoui (2019), ranges from 0.0 to 1.0, where 0.0 corresponds to the unlit moon and 1.0 indicates that the moon is at its brightest (figure 2). Concerning moon phase, the value also ranges from 0.0 and 1.0 (figure 2), where 0.0 corresponds to the new moon; 0.25 to the first quarter; 0.5 to the full moon; and 0.75 to the last quarter (Thieurmel & Elmarhraoui, 2019). The values for the waxing crescent, waxing gibbous, waning gibbous and waning crescent are located between the phases mentioned, without fixed values of reference (Milone *et al.*, 2018; Thieurmel & Elmarhraoui, 2019).

Based on this, we further refined our nighttime-specific subset of location points to include the values corresponding to the illuminated fraction of the moon and moon phase. We then classified the data within this new subset into three groups to better reflect the peak of luminosity associated with each moon phase, where values for the illuminated fraction of the moon corresponding to the first quarter and last quarter are similar and, therefore, included in the same group. The first group includes location points registered under low nocturne luminosity (0.00 to 0.16 of illuminated fraction of the moon, totaling 2,149 location points). The second group includes location points registered under medium nocturne luminosity (0.42 to 0.58 of illuminated fraction of the moon, here corresponding to the first quarter and last quarter given their similar values in terms of illuminated fraction of the moon. The total number of location points was 690). Lastly, the third group includes location points registered under high nocturne luminosity (0.84 to 1 of illuminated fraction of the moon, totaling 3,213 location points).

| Moon phase | Moon phase value | Illuminated fraction value | Representation of the moon |
|---|---|---|---|
| New moon | 0 | 0 – 0.16 | |
| Waxing crescent | - | - | |
| First quarter | 0.25 | 0.42 – 0.58 | |
| Waxing gibbous | - | - | |
| Full moon | 0.5 | 0.84 – 1 | |
| Waning gibbous | - | - | |
| Last quarter | 0.75 | 0.42 – 0.58 | |
| Waning crescent | - | - | |

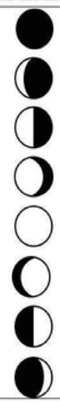

Figure 2 – Variables used to generate subset groups of jaguar's GPS data registered on Pantanal fields to evaluate the potential influence of moonlight on the patterns of space use by the monitored individuals.

## Data analysis

We overlapped each location point with the land cover map of the study area and then extracted the euclidean distance from the forest class. The euclidean distance map (meters) was calculated using raster land cover classification (pixel of 5 m) with start value of reference in the nearest forest habitat. The resulting map included 0 m as a value for the GPS location points inside forests, and higher values, in meters, for location points occurring in fields. Fields showing higher values of euclidean distance were, therefore, considered deeper in our analysis (figure 3). Location points were considered independent since the velocity autocorrelation timescale (h) ranged from 0.2 to 0.5 h for the jaguars monitored (see table 2 in Morato *et al.*, 2016) and we did not include location points with intervals lower than 0.2 h in between them.

To evaluate the potential selection for specific distances in the context of jaguars' use of fields, we compared the GPS locations points obtained via monitoring (figure 1 – D) with random location points. Random points were generated considering all the space available and equal, in numbers, to all true location points of each group of interest (refer to "Moonlight information and selection of jaguars' location data"). The area used for the generation of random points was the same for our three groups of data (i.e. low, medium and high nocturne luminosity), consisting of a 6 km buffer around all jaguar location points registered at night.


Figure 3 – Representation of the gradient of pasture depth, where jaguar location points registered within forests result in forest points with a distance value equal to 0 m whereas points recorded in fields were attributed their specific distance, in meters, from the closest forest edge. Figure scheme elaborated in CorelDRAW Graphics Suite 2020. Forest and pasture vectors elaborated by the authors. Jaguar vector obtained from Vecteezy vector (<a href="https://pt.vecteezy.com/vetor-gratis/guepardo">Guepardo Vetores por Vecteezy</a>).

Given our focus on jaguars' movements in non-forest areas, we only considered location points (both obtained from jaguars' monitoring and random) occurring in fields in our analysis. For each group, the accumulated percentage associated with the depth gradient of jaguars' location points within fields was calculated, as well as the accumulated percentage of random location points. As such, the 'deepest' position (both real and generated) showed accumulated points totaling 100% of location points. The comparison of true vs. random (generated) location points was calculated by the difference observed for the accumulated percentage of points. The greater the difference, the higher the selection for a certain depth (or distance) within fields by the monitored jaguars in relation to distances that they could have explored by chance. To evaluate potential selection, we applied the t-test - an estimate of the probability of the differences observed occurring by chance. The difference was calculated as follows:

$$dif(i) = \%real(i)/\%random(i)*100$$

where (i) represents the depth/distance at every 5 am (minimum raster pixel size).

Finally, distances showing the highest value of dif(i) were identified, indicating the threshold for change in the jaguars' selection pattern under the circumstances studied – i.e. low, medium or high moonlight intensity/nocturne luminosity. Statistical analyses were conducted in the software R.3.3 (R Core Team 2016). Although cloud cover varied within and between nights, its effects on lunar illumination could not be measured. We thus followed Harmsen *et al.* (2011) and assumed cloud cover to only weaken the influence of moonlight on jaguars' movements.

## Results

After discarding the location points registered at night but that occurred within forests, we arrived at 5,197 location points recorded in fields/pastures at night. Therefore, approximately 26.1% of all location points were registered at nighttime and in fields/pastures. More specifically, and considering the values of interest of the illuminated fraction of the moon (figure 2), ~41.3% of jaguars' location points recorded under low nocturne luminosity occurred in fields/pastures – i.e. 888 out of 2,149 location points registered at night, when the moon was visible, and with the associated values of the illuminated fraction of the moon of interest. Under medium nocturne luminosity, 259 out of 690 location points registered at night, when the moon was visible, and with the associated values of the illuminated fraction of the moon of interest occurred in fields/pastures. This corresponds to ~37.5% of location points within the medium moonlight intensity group. Finally, approximately 39.2% of jaguars' location points recorded under high nocturne luminosity occurred in fields/pastures – i.e. 1,258 out of 3,213 location points registered at night, when the moon was visible, and with the associated values of the illuminated fraction of the moon of interest.

Despite maximum distance ranges of approximately 3,000 m being available (figure 4 – A), the greatest difference indicating jaguars' selection for specific depths occurred within the first 100 m from the closest forest edge at nighttime (p-value < 2.2e-16). This difference, in percentage, equals to 31.15% between the accumulated percentage of real location points (62.96%) and the accumulated percentage of random location points (31.81%).

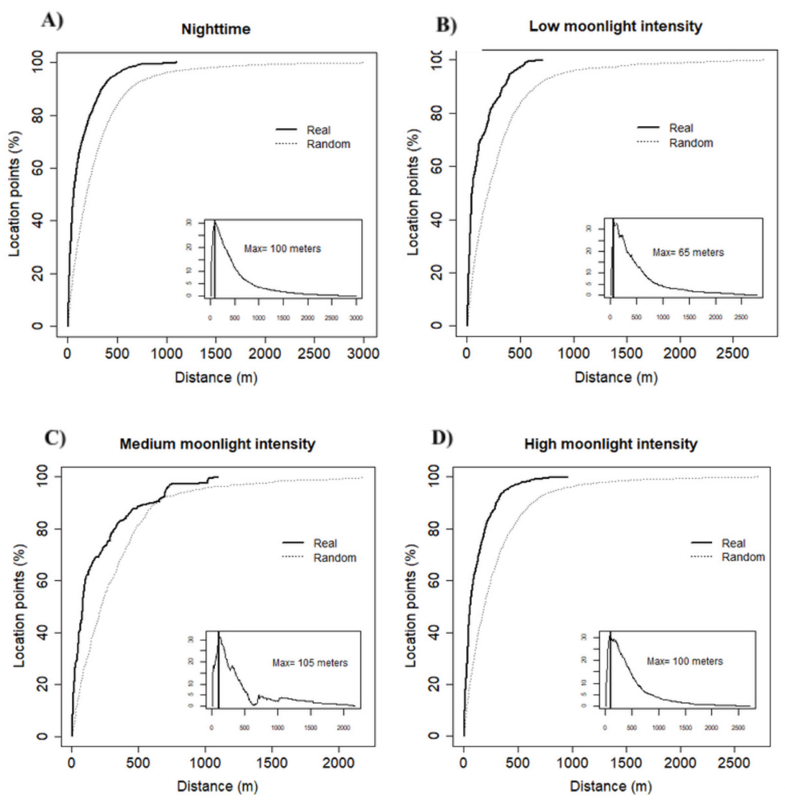


Figure 4 – Accumulated percentages (%) of jaguars' location points in potential pastures in relation to the available distances from forest edges (i.e. pasture depth) in the southern Pantanal at A) nighttime and on nights featuring B) low; C) medium; and D) high nocturne luminosity. Inner charts depicting the maximum distance values resulting from the calculation of the differences between true vs. random accumulated percentages of location points, showing the selection for maximum distances (Max).


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Under low nocturne luminosity (Figure 4 – B) the greatest difference indicating jaguars' selection for specific depths occurred within the first 65 m and equals 33.47%, where 55.97% of jaguar location points were registered within the initial 65 m from the closest forest edge as opposed to only 22.50% of random location points (p-value < 2.2*e*-16). Under medium nocturne luminosity (Figure 4 – C), the greatest difference indicating jaguars' selection for specific depths occurred within 105 m and equals 32.46%, where 61% of true location points were registered within 105 m from the closest forest edge as opposed to only 28.54% of random location points (p-value < 2.2*e*-16). Finally, the greatest difference indicating selection for specific depths occurred within 100 m from the closest forest edge under high nocturne luminosity and equals 31.28% (p-value < 2.2*e*-16). This means that 62.95% of true location points were registered within 100 m on moonlit nights as opposed to only 31.67% of random location points.

## Discussion

Our findings indicate jaguars' selection for distances closest to forests throughout the lunar cycle. The maximum difference observed between real vs. generated location points varied 35 m comparing points registered at nighttime (100 m, Figure 4 – A) and under low nocturne luminosity (65 m, Figure 4 – B) although distances greater than 3 km from the closest forest edge were available. The species' nocturnal movements in fields/pastures in the southern Pantanal seem to be influenced by the extreme in moonlight variation, though not quite as expected. More pronounced evidence of the selection for forest surroundings was found under low nocturne luminosity, contrary to our predictions (55.97% of jaguar location points registered within the initial 65 m from the closest forest edge in low moonlight as opposed to 61% and 62.5% of jaguar location points registered within 105 m and 100 m from the closest forest edge under medium and high nocturne luminosity, respectively – figure 4 – B-D). We anticipated that, similar to what is more commonly observed for lions, lower moonlight intensities would offer better conditions for an inconspicuous species like the jaguar to explore more open areas with potential cattle presence (Oriol-Cotterill *et al.*, 2015; Robertson *et al.*, 2019).

Robertson *et al.* (2019), for example, found that significantly more events of livestock depredation by lions coincided with lower moonlight levels in Botswana, with attacks being more frequent and severe in the dry season. However, the use of pastures by jaguars in our study site seems to better fit Prugh & Golden's (2014) predation risk hypothesis, where species at higher trophic levels are expected to be more active with moonlight as it allows for greater predation success. Although not the focus of our analyses, we recognize that predation dynamics is an important component when assessing the influence of nocturne luminosity on activity, space use and movement patterns of top predators.

Non-specialist top predators like cougars, for instance, show cathemeral activity patterns that are suggested as maximizing the efficiency of their foraging behavior in which they use habitats and the circadian cycle in a more generalist manner, and thus the absence of moonlight influence on their nocturnal activities (Harmsen *et al.*, 2011; Soria-Díaz *et al.*, 2016; Pratas- Santiago *et al.*, 2017; de Matos Dias *et al.*, 2018). But Cavalcanti & Gese (2010) found the occurrence of prey selection by jaguars in the Pantanal, indicating predilection for certain species though they are not necessarily the most abundant. This, together with our findings and the described indirect effect of moonlight on jaguars' activities in Belize and Costa Rica as the result of its direct influence on the activity of their prey species (Harmsen *et al.*, 2011; Montalvo *et al.*, 2020), point to the need of further investigating the predation dynamics of jaguars under varying moonlight luminosity in the southern Pantanal to better understand the species' response to the lunar cycle. Bearing that in mind, we suggest the possibility that jaguars move slightly deeper in pastures on moonlit nights because their wild prey in forests could better detect them with higher nocturne luminosity (see Prugh & Golden's (2014) visual acuity hypothesis). However, Prugh & Golden (2014) describe that the suppressive effect of moonlight on prey activity patterns is usually stronger in more open habitat (habitat-mediated predation risk hypothesis). In any case, the opportunistic nature of jaguars' hunting behavior has been demonstrated as playing a role in increased rates of cattle depredation in the Pantanal in response to other changing environmental factors like flood pulse (e.g. Cavalcanti & Gese, 2010; Tortato *et al.*, 2015). As the monitored jaguars at our study site do not travel far into pastures in any luminosity context but slightly deeper on moonlit nights, perhaps increasing moonlight brightness might aid the species' stalking and ambush of livestock where peripheral vegetation functions as shelter (Balbuena-Serrano *et al.*, 2020).

Predators may show different behaviors in different phases of the moon, adapting activities that are more suited to the available light (Preston *et al.*, 2019). Thus, future investigations on the influence of moonlight on jaguars' activity patterns in the Pantanal could explore the species' behavior within and outside forests combining GPS tracking, camera traps, and predation records.

There are already documented differences concerning males vs. females in terms of jaguars' habitat selection and use in the Pantanal, as well as individual preferences in terms of prey selection (Cavalcanti & Gese, 2010; Morato *et al.*, 2016; Morato *et al.*,2018; Kanda *et al.*, 2019). As we did not account for potentially different responses to moonlight based on sex or individual preferences due to limited data available (see table in supplementary material), future studies could compare and contrast males vs. females in terms of behavioral responses to moonlight variation, and also consider individual preferences.

Furthermore, the influence of moonlight on the responses of species that show variation in color poses interesting questions for future studies. San-Jose *et al.* (2019), for example, found that barn owls (*Tyto alba*) are differently affected by moonlight based on the coloration of their plumage. Graipel *et al.* (2019) point to the evolutionary dilemma of melanistic felid predators being almost invisible at night, but unable to communicate well with conspecifics at low levels of light which may, for example, hinder the survival of cubs of melanistic mothers. In this context, whether melanistic individuals of *Panthera onca* are affected by moonlight differently in comparison to the effects observed in non-melanistic individuals emerges as yet another avenue for investigation.

With regards to the concept of landscapes of fear and the downgrading of large carnivores from ultimate to penultimate predators by humans (see Oriol-Cotterill *et al.*, 2015), Robertson *et al.* (2019) and Orion-Cotterill *et al.* (2015) elaborate on the spatiotemporal partitioning of lions' activities in a way that minimizes the risk of human-caused mortality while maximizing the use of human-dominated landscapes. At our study site, the habituation of jaguars to ecotourism activities implies that human presence is most likely not perceived as a threat by them (refer to https://oncafari.org/en/our-work/ecotourism/). As this reflects the exception as opposed to the rule in terms of felids in general, especially the jaguar (Morato *et al.*, 2018; Macdonald, 2019; Romero-Muñoz *et al.*, 2020), future studies could focus on the role of human presence in jaguars' nocturne behaviors and whether moonlight mediates responses. Although not accounting for the potential influence of the lunar cycle on this relationship, Smith *et al.* (2017) explore how the fear of the human 'super predator' alters the feeding behavior of cougars, with potential to result in human-induced trophic cascades.

Limitations in our study emerge from our approach not taking into account flood pulse, nor the different characteristics of fields in the Pantanal (i.e. dry or humid, open or vegetated). This was due to insufficient data, including the availability of satellite imagery of the study site during the wet season with fine resolution allowing for land cover mapping plus detailed flood pulse data of the study area during the monitoring period of the tracked jaguars; and a suitable number of jaguars' location data meeting the selection criteria (see Material and Methods) allowing for refined investigations considering field-specific characteristics. These environmental and landscape variables likely play a role in the behavioral and space use responses of jaguars to changing moonlight brightness and should be further investigated in future studies.

Finally, our study not only is the first investigation of moonlight influence on jaguars' space use in the Pantanal, but it also points to the preference of jaguars for forest areas as already documented (most recent literature on the Pantanal from Zeilhofer *et al.* (2014), Morato *et al.* (2016), Morato *et al.* (2018), Kanda *et al.* (2019)). Close to 60% of location points registered at night in either of the three groups of nocturne luminosity analyzed occurred in forest areas, which in turn cover only 30% (approximately) of our study site. In light of Miranda's *et al.* (2018) gloomy prediction of increasing human-driven transformations in the Pantanal landscape in the near future, we can


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expect the population of jaguars in this system to suffer dramatically. We have witnessed clear signs of this recently, when by early October 2020 at least 22% of the Brazilian Pantanal had burned taking into account 2020 fires solely (Einhorn *et al.*, 2020). Unless this transformation trend is reverted, there is the likelihood of increasing events of livestock depredation by jaguars as wild prey succumb.

## Conclusion and Recommendations

Knowledge on the environmental factors that may contribute to cattle depredation by jaguars emerges as crucial for the development and implementation of mitigation measures. We found that although jaguars remain within ~100m from forest edges throughout the lunar cycle, they tend to venture deeper in pastures under medium to high moonlight illumination in our study area. This information is useful for the design of cattle management practices. Hence, we recommend that not only the composition of herds should refrain from high concentration of juveniles (Tortato *et al.*, 2015), but also that herds should be protected (e.g. fences) and kept away from forest edges at all times, acknowledging that brighter nights during the dry season may pose additional threat to domestic animals once Cavalcanti & Gese (2010) reported higher cattle depredation rates under such seasonal conditions. Furthermore, following Miller's (2015) 'six-step process of creating and applying predation risk maps to mitigating human – carnivore conflict' (Figure 3 in Miller (2015)) is highly advisable. This is so because the variation in predators' hunting success over time is likely to affect the spatiotemporal distribution of prey species, and therefore the spatiotemporal characterization of hunting that can influence the wider ecosystem as well as patterns of human–wildlife conflict (Preston *et al.*, 2019).

At the higher level, and in order to change the current status of terrestrial mammals including jaguars, Macdonald (2019) suggests 'transdisciplinary conservation' as a holistic approach that places conservation in the wider context of the human enterprise, embracing everything "from groundedness to geopolitics" (p. 64). Indeed, Romero-Muñoz *et al.* (2020) emphasize the need for holistic approaches that consider the connections between agricultural expansion, agricultural trade and other threats such as wildlife trafficking for the effective conservation of South America's most emblematic predator. In this regard, growing attention should be dedicated to biodiversity conservation in the context of the sustainable development of social-ecological systems, and the work of Tomas *et al.* (2019) has set the stage for this to happen in the Pantanal. They identified multiple ongoing threats as well as means to tackle them, highlighting that there is still much to be done in the sense of sustainability efforts finding their way into decision-making, policies, laws, and practices in the region. We hope our modest contribution in illuminating nocturnal jaguars' movements in the Pantanal to aid the development and implementation of cattle management practices that reduce the likelihood of livestock depredation, highlighting the urgency in addressing jaguars' habitat loss and modification, ultimately contributing to the mitigation of retaliatory killing.

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# Supplementary Material

Supplementary Table 1 – GPS data collection schedule and location points

| | | | | | Location points considered for analysis | | |
|---|---|---|---|---|---|---|---|
| **Sex** | **ID** | **Monitoring period (dd/mm/yyyy)** | **Location scheme** | **Total location points registered** | **Low nocturne luminosity** | **Medium nocturne luminosity** | **High nocturne luminosity** |
| female | Chuva | 30/10/2011 – 27/01/2012 | I | 852 | 40 | 23 | 101 |
| male | Nati | 01/11/2011 – 23/12/2011 | I | 1,065 | 41 | 22 | 80 |
| male | Brazuca | 04/04/2012 – 16/04/2012 | II | 198 | 0 | 10 | 19 |
| female | Vida | 04/06/2012 – 19/06/201 | II | 211 | 0 | 5 | 8 |
| female | Esperança | 22/10/2012 – 06/11/2013 | II | 6,373 | 278 | 59 | 327 |
| female | Teorema | 16/04/2013 – 21/01/2014 | II | 4,931 | 250 | 52 | 329 |
| male | Brutus | 19/10/2013 – 03/01/2014 | II | 1,339 | 54 | 12 | 66 |
| female | Troncha | 22/10/2013 – 17/01/2014 | II | 1,421 | 53 | 20 | 96 |
| female | Natureza | 27/10/2013 – 13/05/2014 | II | 3,519 | 172 | 56 | 238 |
| | | | Total: | 19,909 | 888 | 259 | 1,258 |

Jaguars' IDs, monitoring period, and transmission scheme (I = every hour; II = every 2h between 5am and 3pm, every hour between 15pm and 5am). Location points considered for data analysis selected according to the criteria described in 'Moonlight information and selection of jaguars' location data' and 'Data analysis' sections of Material and Methods.

## Supplementary Material – Mapping

Digital manipulation of satellite imagery was performed using ArcGIS 10.1 (Environmental Systems Research Institute – ESRI, 2012) and GRASS GIS (Geographic Resources Analysis Support System – GRASS). The spatial structure of the landscape was characterized via mapping based on four RapidEye satellite images (2129817 from 24/06/2012; 2129918 from 23/06/2012; 2129818 and 2129917 from 02/07/2012) with spatial resolution equal to 5 m. These images were provided by the Brazilian National Research Center for Carnivores Conservation (CENAP/ICMBio). We also used one Landsat 5 image (226/074 from 29/09/2011), with spatial resolution equal to 30 m, obtained from the Brazilian National Institute for Space Research's website (INPE – http://www.inpe.br/).

Mapping was done via supervised classification utilizing the maximum likelihood estimator. For each satellite image, we extracted ten samples for every class of land cover that worked as examples. We defined six distinct classes: water bodies, forest, dry field/pasture with trees, dry field/pasture without trees, humid field/pasture with trees and humid field/pasture without trees. Subsequently, we worked on the refinement of the polygons and classes according to the scale (cm) 1:15,000. Since we did not consider the different characteristics of the fields in our study site for our analysis, we grouped all fields into a single 'fields' class. The original land cover classification map can be found below.

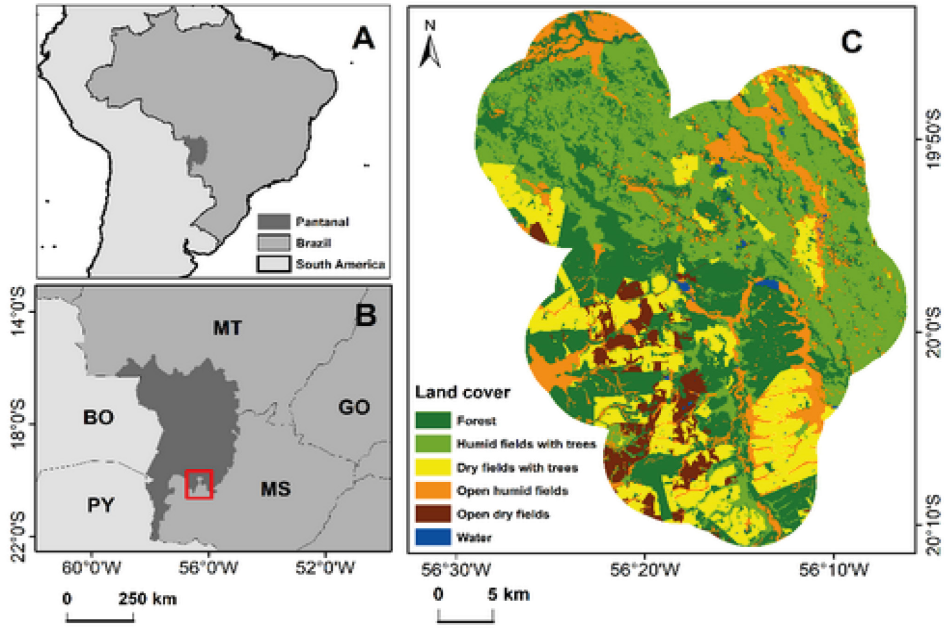


Figure 1 – Study area at the Caiman Ecological Refuge and surroundings, located in Miranda – MS, Brazil; A) Pantanal region (dark gray) within the Brazilian territory (medium gray); B) Red rectangle indicating our study site in the Pantanal region, Brazil; C) Map of land cover classification of the study area. Area depicted originating from a 6km buffer based on all GPS location points of collared jaguars. Most of the study area (total ~131.65 thousand ha) corresponds to humid fields with trees (~35%, 46.2 thousand ha in light green), followed by forest areas (~30%, 39.4 thousand ha in dark green) and other types of land cover such as dry fields with trees (~16.5%, 21.7 thousand ha in yellow), open (without trees) humid fields ( ~13%, 17.2 thousand ha in orange), open dry fields (~5%, 6.3 thousand ha in brown), and water bodies (~0.5%, less than 1 thousand ha in blue).

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