acta ethologica
https://doi.org/10.1007/s10211-023-00425-5

ORIGINAL PAPER

Safe in the heights: trees as safer sites for female jaguars and their cubs in the Pantanal

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Received: 28 October 2021 / Revised: 24 May 2023 / Accepted: 6 June 2023

Abstract

While the use of trees has been widely documented for most of the big cats, this information is scant for the jaguar (*Panthera onca*). In this study, we investigated the use of trees by jaguars, evaluating different underlying reasons as well as the frequency of tree use based on sex, age, and reproductive status. Data were obtained from 2013 to 2020 through a combination of direct observations during fieldwork and camera trapping focused on this behavior in the Brazilian Pantanal. We documented 252 climbing events (176 direct observations, 76 camera captures). Using only camera trapping data to avoid observers' influence on jaguar behavior, we fitted generalized linear mixed models (GLMM) with jaguar identity as a random factor to test the effects of age, sex, and presence of conspecifics in the odds of animals climbing trees. We also used a generalized linear model (GLM) to test the effect of adult body weight on jaguar tree climbing probability. Age and presence of conspecifics were the most important drivers of jaguar climbing behavior in the study area, with cubs being more likely to climb trees than adults of either sex (odds ratio = 7.91, $p < 0.001$), and the presence of conspecifics, irrespective of age and sex, accentuated that behavior (odds ratio = 3.26, $p < 0.005$). Adult females (especially the lighter ones) and cubs were commonly recorded through direct observation on trees, a similar trend to our GLMM that showed a marginally negative effect of body weight on jaguar tree climbing probability. Only a few adult male jaguars ascended trees, and in all cases, these males were following females in heat. We suggest that trees are vertical extensions inside jaguar home ranges and may be safe refuges for resting and for protecting offspring against potential threats, including the harassment of large adult males.

Keywords Behavior · Ecology · Felidae · Pantanal · *Panthera onca* · Wild cat

Introduction

Big cats can climb trees, and among large felid species, leopards (*Panthera pardus*) are most known to do so, hunting and managing to stash their prey on trees (Sunquist and Sunquist 2002). Selective pressure may have favored the development of this behavior in leopards because it minimizes kleptoparasitism by dominant competitors, such as lions (*Panthera leo*), hyenas (*Crocuta crocuta*), and tigers (*Panthera tigris*) (Stander et al. 1997; Karanth and Sunquist 2000; de Ruiter and Berger 2001). Leopards can also use trees as a refuge after being detected by competitors (Rafiq 2016) and for scent marking behaviors (Bothma and le Richet 1995). Cheetahs (*Acinonyx jubatus*), especially territorial males, use "play trees" for scent marking as part of their communications and territorial marking (Marker-Kraus et al. 1996). Serengeti lions climb trees to play, lie on the broad horizontal branches, scan the landscape looking for preys, or escape from harassment of buffalos (*Syncerus caffer*) and hyenas (Schaller 1972).

Although there are anecdotal reports about jaguars (*Panthera onca*) hiding in trees from hunters, little is known about tree use by the largest cat of the Neotropics

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Published online: 15 June 2023

throughout most of its range, with few previous records of tree use in threatening or stressful situations (Almeida 1990; Rampim et al. 2020). A recent study in a seasonally inundated island in the Amazon forest, however, has brought strong evidence of jaguars living an arboreal lifestyle during the three to 4-month-long wet season when the waters rise more than 10 m (Ramalho et al. 2021). In that region of the Amazon, the high canopy is the only dry ground available over ~ 11,000 km^2 forcing jaguars to climb trees and prey chiefly on arboreal mammals such as brown-throated sloths (*Bradypus variegatus*) and red howler monkeys (*Alouatta juara*) (Rabelo et al. 2019). Unlike the extensive and continuous flooded forests present in large portions of the Amazon, the Pantanal biome is characterized by a mosaic landscape composed of open grasslands, marshes, savannas, and forests, presenting subtle differences in relief that regulate the flood during the 6-month-long wet season. Most tracts of forest stand higher than open habitats, and hence, the water level differs from around 1.5 m to as low as a few centimeters inside the forests (Gonçalves et al. 2011), which means that wildlife can still move widely around the landscape. In this seasonally flooded savannah, jaguars wander through both open and closed habitats all year round, and direct observations of jaguars climbing trees in our study area have raised some questions regarding factors that drive this behavior. Another striking distinction between Amazonian and Pantanal jaguars is related to their sizes, with the latter attaining much heavier body masses (Azevedo and Murray 2007; Ramalho et al. 2021).

Intraspecific killing (Azevedo et al. 2010) and infanticide (Soares et al. 2006; Tortato et al. 2017) may pose important threats to breeding females and their dependent young, forcing the need to find safe sites to increase survival chances of young until independence. For instance, female leopards can use abandoned aardvark (*Orycteropus afer*) burrows to protect their cubs (Steyn and Funston 2009). Female jaguars with cubs may shift their movement pattern to minimize the chance of encounters with potential infanticidal males, as hypothesized by Foster et al. (2010). In this scenario, trees may serve as safe shelter for the most vulnerable age-sex classes against the harassment and intraspecific killing by adult males, which are considerably larger than adult females throughout the species' distribution (Seymour 1989) and may find more difficulties to climb and move on trees.

Here, we report the findings from the first systematic study of tree use by jaguars in the Brazilian Pantanal, the world's largest freshwater wetland. We carried out surveys through field observations and camera trapping to (1) evaluate the frequency, activity patterns, and duration, (2) find the drivers associated with jaguar tree climbing behavior, and (3) better understand the individual characteristics of jaguars climbing trees (sex, age, and reproductive status). We used camera trap data and direct observations to test the hypothesis that in the Pantanal biome, trees may serve as safe refuges used by vulnerable sex-age classes to avoid harassment of large adult male jaguars. We expected to record cubs climbing trees more often than adults of either sex; adult males climb trees less frequently than adult females or cubs, and females with dependent young climb trees more often than lone adult females.

Methods

Study area

Caiman Ecological Refuge (CER) is located between the municipalities of Miranda and Aquidauana, Mato Grosso do Sul, Brazil, predominantly in the Pantanal but with some areas in Cerrado biome (Kanda et al. 2019). The landscape is composed of a mosaic of vegetation types, including exotic (e.g., perennial tropical grass *Urochloa humidicola*) and native pastures, dense forests, and patches of many different sizes of forest vegetation in a matrix of savannah grasslands. Much of the area is flooded during the rainy season (December–April). The CER is a ranch and nature reserve that stretches across ~ 530 km^2 and has been raising cattle since 1916 and added wildlife tourism to the economic activities in 1987. Research and tourism focused on jaguars began in 2011. Previous studies have estimated a density of 6.5–7.0 jaguars per 100 km^2 in the region (Soisalo and Cavalcanti 2006; Azevedo and Murray 2007).

Data collection

Direct observations

From 2013 to 2020, direct observations of jaguars using trees and additional information such as date, time, location, and tree species (if possible) were recorded. The direct observations occurred during (1) GPS monitoring and tracking of collared jaguars, (2) active search (e.g., following footprints and spotlighting), (3) tour activities with tourists, and (4) opportunistic encounters. Jaguars were identified to the individual level whenever possible, according to their unique rosette pattern.

Camera trapping

To evaluate if tree climbing is related to jaguar sex, age, and reproductive status, we monitored 18 trees using 36 trail cameras (Bushnell, Trophy Camera HD Brown–119876, Overland Park, Kansas, USA) from November 2018 through January 2020. Trees were selected based on previous sightings and/or signs of usage, such as claw marks, totalling five different tree species: fig tree (*Ficus* sp.), Tarumã tree

(*Vitex cymosa*), pacara earpod tree (*Enterolobium contortisiliquum*), yellow trumpet tree (*Tabebuia alba*), and cabbage tree (*Andira inermis*). Half of the cameras were set on the ground, pointing in the direction of the trunk. The other half were attached to a main branch up in the tree (most likely to be used by jaguars) using a portable ladder with a maximum height of six meters (the chosen branches did not exceed this height) and climbing equipment. Cameras were deployed to record and individualize jaguars that could potentially climb trees, as well as to estimate the activity pattern and the duration that individual animals stayed on trees. The cameras were set to record 15 s at an interval of 0.6 s between recordings. They were checked every 2 months to download the recorded videos, change batteries, and assure proper functioning of the camera. All videos were stored in the project database, and the jaguars recorded were identified to the individual level. Five cameras were damaged by animals (e.g., cattle, capuchin monkeys, and woodcreepers) and three cameras burned during a fire in August 2019 that devastated around 300 km^2 of the study area, causing the lack of data from two trees, which were removed from the analysis. The other cameras were replaced to continue the study.

We considered as a climbing event when the animal was recorded above the first trunk bifurcation and/or at the branches, considering independent events after 60 min of the previous one to avoid autocorrelation (Foster et al. 2013). If the same animal stayed up in the tree for more than 60 min, we considered it as a single event. The sex of individuals was recorded, and animals were classified as adults (independent from the mother) or cubs (animals still dependent on the mother's care). Adult females were also classified in relation to their reproductive status as "mother" (with dependent cub) or "single" (no dependent cub) to test if the presence of cubs influences their climbing behavior. The presence of a conspecific (including cubs) was registered using binary code for "presence" and "absence" (1 and 0, respectively).

For 19 of the 37 individuals recorded in this study, we obtained exact weights after chemically restraining the animals for other scientific purposes not directly related with this study (e.g., biometry, collaring, and collecting biological samples). Then, we used this information to assess the effect of body mass on tree climbing behavior in jaguars (Online Resource 1 – Fig. S1).

Data analysis

To test the hypothesis that trees may serve as safe shelter against potential harassment of large adult males, we developed generalized linear mixed models (GLMM; Zuur et al. 2009) with a binomial distribution where independent climbing events detected by camera traps were the response variable and sex (i.e., male or female), age (i.e., adult or cub), and presence of conspecifics were the independent variables (Online Resource 1 – Table S1). Furthermore, to test whether females with dependent cubs were more likely to climb trees than females without cubs, we developed a GLMM using data only for climbing events of adult females using the presence of cubs as the moderator variable. For the purpose of these analysis, we chose the camera trap data to avoid any bias caused by the presence of observer as a factor to drive jaguars to climb trees. For controlling the possible effect of individual's behaviors, the identity of jaguars entered the models as a random factor. We used Akaike's information criteria controlled for small samples (AIC_C) to select the most parsimonious models (Burnham et al. 2011). To disentangle the effect of body weight and sex on jaguar climbing behavior, we have built a GLMM with a binomial distribution, including jaguar identity as a random effect, testing independent climbing events against body mass measured in kilogram. For this model, we have used only camera trap records of jaguars that we had exact data on body mass ($n = 15$). Furthermore, we also ran a generalized linear model (GLM) using the previous formulation without jaguar identity as a random factor, because we were expecting the loss of predictive power due to less degrees of freedom and fewer individuals with known weights (Online Resource 1 – Table S1, Fig. S1). All analyses were performed in R (R Core Team 2021), using the packages *lmer* (Bates et al. 2015) and *AICcmodavg* (Mazerolle 2020).

Results

Altogether, we observed a total of 252 independent tree climbing events, 176 detected by direct observations and 76 by camera traps (Table 1). Records of adult females with cubs represented 39.68%, followed by records of adult females without cubs (37.70%) and with cubs (20.64%). Only five records of adult male jaguars ascending trees were recorded in this study, representing only 1.98%.

Table 1 Records of jaguars ascending trees separated by sex-age classes. Records of adult females were distinguished between "mothers" (with cubs) and "singles" (without cubs)

Class	Direct observation	Camera trap	Total
	n (%)	*n (%)*	*n (%)*
Adult males	4 (2.27)	1 (1.32)	5 (1.98)
Adult females	88 (50.00)	7 (9.21)	95 (37.70)
without cub	67 (38.07)	33 (43.42)	100 (39.68)
Adult females	17 (9.66)	25 (32.89)	42 (16.67)
with cub	0 (0.00)	10 (13.16)	10 (3.97)
Female cubs			
Male cubs			
Total	**176 (100.00)**	**76 (100.00)**	**252 (100.00)**

Direct observations

From a total of 3,951 field observations, jaguars (three males and 15 females) were recorded ascending trees in 4.45% ($n = 176$) occasions on 144 different days. On four occasions, we observed adult males climbing trees; in three cases, they were following females to stay together with their mating pairs. In one case, a male that was tracking the odor of a female in heat climbed a tree, sniffed some branches for less than 3 min, and climbed down. Adult females (with and without cubs) were seen 155 times in trees. Although we did not carry out a systematic behavioral survey during the direct observations, we can state that most times (~ 80%) they were predominantly resting up in the trees. In eight, they were mobbed or ran away from white-lipped peccaries, and in three, they escaped from harassment of the cattle. In 15 events, females climbing trees were related to mating behavior, with males waiting under the trees in 11 cases. On two occasions, two different females were seen climbing trees in an attempt to catch coatis (*Nasua nasua*), a semi-arboreal prey. Regarding the females with cubs, on nine occasions, they were seen climbing trees accompanied by their offspring. Cubs were observed climbing trees 17 times, and on five occasions, they were without their mothers. Considering all jaguars recorded through direct observation, we found individual variation in the frequency of tree climbing behavior, with some individuals climbing trees more frequently than others (range = 1–125). One female jaguar accounted for 58.8% of all direct observations.

We identified jaguars climbing ten different tree species. Fig trees (*Ficus* sp.) and Tarumã (*Vitex cymosa*) represented 35.4% and 25% of the observations (when the tree species was known), with nine and eight jaguars climbing them, respectively (Table 2).

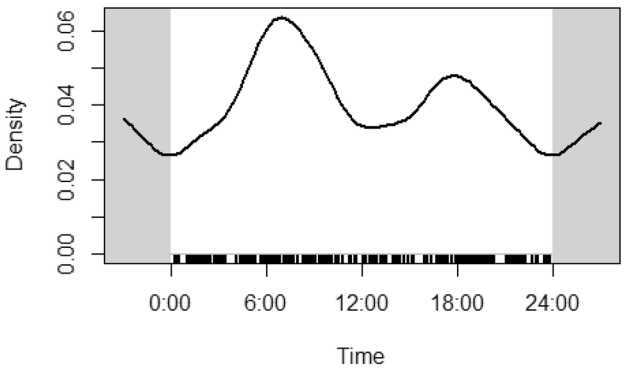

Fig. 1 Density plot of jaguar activity from camera trap data. Original records presented as a rug along the "time" axis

Camera trapping

Camera traps recorded 63,950 videos, 1,031 of jaguars (257.75 min). The 1,031 videos resulted in 76 independent records of individual jaguars climbing trees (Online Resource 1) and 168 independent records of jaguars not climbing. In total, 31 different individuals were filmed (20 females and 11 males). Twelve of them were recorded climbing trees, representing 45.7% ($n = 471$) of the videos. Eight adult females were recorded climbing trees in 40 events, while three cubs were filmed on trees in 35 occasions. There was only one record of an adult male climbing a tree (three sequential videos), sniffing the trunk and branches for more than 6 min. This event occurred 7 days after an adult female had climbed up the same tree for three consecutive days. Of the 76 tree climbing events, 44.7% took place between 05:00 and 09:59 h (Fig. 1), showing that jaguars climbed trees more often during the morning. In 73 events, it was possible to estimate the duration. Cubs and females with

Table 2 Species of trees used by jaguars through observation data

Tree species	Events	Trees (*n*)	No. of jaguars
Fig tree (*Ficus* sp.)	34	25	9
Tarumã tree (*Vitex cymosa*)	24	24	8
Genipap tree (*Genipa americana*)	14	3	1
Pacara earpod tree (*Enterolobium contortisiliquum*)	8	3	3
Sandpaper tree (*Curatella americana*)	6	5	3
Trumpet tree (*Tabebuia* sp.)	4	4	1
Yellow trumpet tree (*Tabebuia alba*)	3	2	3
Barreiro tree (*Machaerium* sp.)	1	1	1
Mango tree (*Mangifera indica*)	1	1	1
Pink trumpet tree (*Tabebuia heptaphylla*)	1	1	1
Not identified	80	-	14

Table 3 Time spent (minutes) by jaguars on trees based on sex-age classes estimated from camera trap data

Class	Events (individuals)	Time spent on trees (min)
Adult male	1 (1)	6.26 ± 0.00 (6.26–6.26)
Adult female without cub	3 (3)	0.73 ± 0.79 (0.1–1.6)
Adult female with cub	36 (5)	51.31 ± 50.52 (0.23–168.76)
Cub	33 (3)	28.95 ± 32.41 (0.10–133.46)

cubs spent longer times up in trees (Table 3). Among the 18 trees monitored with camera traps, five trees were not climbed by jaguars.

Models

Two of our GLMMs were equally plausible (ΔAICc < 2) and included age and presence of conspecifics as important moderators, and sex was also included by the top model (Online Resource 1 – Table S2), showing that age and presence of conspecifics are important drivers of climbing behavior of jaguars in the study area. Cubs are more likely to climb trees (odds ratio = 7.91, $p < 0.001$) than adults of either sex, while adult males are less likely to do so (odds ratio = 0.17, $p = 0.08$) compared to the other age-sex classes (Table 4, Online Resource 1 – Tables S2, S5 and S6). The presence of conspecifics, irrespective of age and sex, was also important and accentuated climbing behavior (odds ratio = 3.26, $p < 0.005$; Table 4, Online Resource 1 – Tables S2, S5 and S6). Looking only at adult females, the presence of cubs seems to influence their climbing behavior, but the difference was not significant (odds ratio = 2.49, $p = 0.1$, Table 5, Online Resource 1 – Tables S3 and S5). Regarding the effect of body weight on jaguar climbing behavior, our GLMM showed a marginally significant negative effect ($p = 0.08$), while the GLM detected a significant negative effect (Online Resource 1 – Fig. S2).

Discussion

To our knowledge this is the first study to systematically record tree climbing by jaguars in the Pantanal and to evaluate factors that favor this behavior. Considering the comparatively high number of records and the larger amount of time of mothers and cubs on trees, this behavior may be a strategy to increase the cubs' survival during the first months of life. Infanticidal behavior by adult males has been previously reported for jaguar (Soares et al. 2006), as well as for other big cats, such as cougar (*Puma concolor*) (Logan and Sweanor 2001) and other *Panthera* species (e.g., tigers (Goodrich et al. 2008), lions (Schaller 1972; Pusey and Packer 1994), and leopards (Bailey 1993; Balme et al. 2013)). To deal with this potential threat, female jaguars can display mating behavior during cub rearing to minimize the chances of infanticide perpetrated by adult males (Fragoso et al. 2023). Therefore, use of trees as safer refuges to hide and protect vulnerable cubs from harassment and infanticide by adult males is an additional counterstrategy used by females. Trees could also protect the fragile cubs against other threats such as possible terrestrial predators or other

Table 4 Results (odds ratio) of the null model against the best ranked model where age and sex of jaguars affect the chances of an animal climbing a tree. Models' information: response variable (climbed); type, mixed effects generalized linear regression; error distribution, binomial; link function, logit

	Models	
Fixed effects	**Age-sex presence**	**Null**
Intercept	0.09 [0.03, 0.33]***	0.51 [0.39, 0.66]***
Age-cub	7.91 [1.65, 38.00]**	
Sex-male	0.17 [0.02, 1.26]	
Presence-yes	3.26 [1.46, 7.26]**	
Random effects		
Group	Parameter	SD
ID	(Intercept)	1.68
Observations	253	253
AIC_C	259.05	278.43
AIC_C weight	0.54	0.00
Pseudo R^2	0.58	0.00

$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Table 5 Results (odds ratio) of the null model against the model testing the effect of the presence of cubs in climbing behavior of adult females. Model information: response variable (climbed); type, mixed effects generalized linear regression; error distribution, binomial; link function, logit

	Model	
Fixed effects	**Cub**	**Null**
Intercept	0.11 [0.02, 0.49]**	0.09 [0.02, 0.51]**
Presence of cub	2.49 [0.84, 7.43]	
Random effects		
Group	Parameter	SD
ID	(Intercept)	1.88
Observations	149	149
AIC_C	155.66	157.01
Pseudo R^2	0.53	0.57

$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

aggressive species incapable to climb, such as white-lipped peccaries (e.g., Rampim et al. 2020). So, the learning process of the cubs may also be important for their own survival.

In 18 occasions, females were also recorded climbing up in the presence of their mates in an attempt to temporarily "escape" and rest, while the males usually waited under the trees or spent time marking the surrounding vegetation. This may indicate that the presence of a mate can be an influencing factor, prompting females to ascend trees, especially the heavier ones that are rarely recorded in other contexts. In our study, adult male jaguars climbed trees only on rare occasions, mostly in the pursuit of females for mating, suggesting that reproduction purposes may drive this behavior in males. Schaller (1972) observed that male lions in Serengeti ascended trees proportionally less often than females and cubs.

Although the GLM confirmed our hypothesis that body size is an important factor for the frequency of tree climbing, when the identity of jaguars was included in a GLMM, the effect became marginally significant. This is very likely due to the resulting reduction of degrees of freedom and for the fact that many individuals with known weight have few observations each. Three adult female jaguars ranging from 54 to 70 kg indeed were more likely to climb trees than any other jaguar, and they were responsible for 53% of the 129 observations. Adult male jaguars in our study area are significantly heavier than adult females (range = 102–140 kg and 51–100 kg, respectively), which means 36.5% of difference in mean weight. In this scenario, larger individuals are at higher risk of damaging from a tree fall, because some branches cannot resist their weight, so lighter individuals may be safe from predation when moving through branches where larger males cannot access without risking a fall. Indeed, there was only one observation of an adult male jaguar (107 kg) climbing a tree, which had been used a few days earlier by an adult female for consecutive days.

In a seasonally inundated forest in Amazon, both male and female jaguars adopt a semi-arboreal lifestyle, but in this area, adult female jaguars weighed 40–50 kg and males 50–60 kg (Ramalho et al. 2021), which are indeed in the lower range of adult weights for Pantanal jaguars. This is a morphological trace that would make it difficult for large Pantanal jaguars climb trees higher than 30 m as Amazon jaguars do (Ramalho et al. 2021). Furthermore, while the water column in the Amazon region reaches > 10 m in depth (Ramalho et al. 2009), in our study site, it reaches less than 0.5 m (Fragoso CE, personal observation), which means that wildlife can still move widely around the landscape, and hence, it is unlikely that the flood pulse is an important driver of jaguar tree climbing behavior in the Pantanal.

The adaptation to have a periodic arboreal and semi-aquatic existence also depends on food resources during flood periods, and in Mamirauá, it is reported a high abundance of sloths and other arboreal mammals (Queiroz 1995), important prey for this big cat (Ramalho 2012). In our study area, there is no occurrence of sloths (*Bradypus* spp.), and there is a low availability of semi-arboreal prey species. As a consequence, arboreal and semi-arboreal prey species appear less important in jaguars' diet, representing only 0.9% of coatis, 5% of southern tamanduas (*Tamandua tetradactyla*), and no primates (Fragoso CE, unpublished data). In the Pantanal, jaguars concentrate on caimans (*Caiman yacare*) and capybaras (*Hydrochoerus hydrochaeris*) as wild preys, which make up 45.8% and 14.8% of their diet at our study site, respectively (Fragoso CE, unpublished data).

Our results show that only one female accounted for more than half of the direct observations. But this specific jaguar is very habituated and easily located through the GPS/VHF collar, allowing long periods of direct observations and being one of the most seen individuals in the study site. This suggests that it is more related to an artifact of our visual monitoring than a specialization in tree climbing for some individuals.

The preference for fig trees and Tarumãs could be explained by the fact that both are common in the region, leafy, with many horizontal branches, providing shade, coverage, and comfortable places to rest. In addition, the structure of the fig trees (usually an unevenly growing trunk with ramifications that form low branches) can also facilitate the climbing of the cubs. Most of the Tarumã trees found in the study area are marked by clawing, probably because this species' bark is soft, allowing jaguars to clean their claws while leaving a visual and olfactory marking.

Comparing our results with the available literature (Ramalho 2012; Ramalho et al. 2021), several variables may drive the tree climbing behavior in different places. This may be explained by the differences in the flood regimes, prey availability, body sizes, ecology, and evolution of the species to survive in areas under different conditions and landscapes. In addition to provide vegetation cover, an important environmental factor for this species (Morato et al. 2018), trees seem to be a vertical extensions of jaguars' home ranges. Our findings show that in our study area, trees may act as safer places for the protection of more vulnerable age-sex classes against infanticide and harassment perpetrated by adult males and aggressive preys.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10211-023-00425-5.

Acknowledgements Special thanks are due to Caiman Pantanal for allowing this long-term jaguar conservation project, to Log Nature and Bushnell Corporation for the technical support in this study, to Onçafari team members (https://oncafari.org/), and to Érica Rosa for the help during the fieldwork. The authors also thank Arthur Fernandes and Wellyngton Espíndola Ayala for the statistical analysis, Peter Leimgruber and Ronaldo Gonçalves Morato for reviewing this paper, and Felipe Soares Bufalo for the first conversations about the analysis. HVBC has a scholarship granted by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil.

Author contribution Carlos Eduardo Fragoso: Conceptualization, methodology, formal analysis, investigation, resources, writing—original draft, writing—review and editing, funding acquisition.

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Mario Haberfeld: Resources, writing—review and editing, funding acquisition.

Henrique Villas Boas Concone: Methodology, formal analysis, writing—review and editing.

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Funding Our project was funded by the National Geographic Society, through the Early Career Grant (reference number EC-414R-18).

Data availability All data analyzed during this study are included in this published article and its supplementary information files. Additional tables showing the distinct models, hypothesis, and predictions, as well as the model parameters, respective AICs, and model estimates, are presented in Online Resource 1. A compilation of camera trap videos is presented as Online Resource 2.

Declarations

Ethics approval All the captured procedures followed the guidelines of American Society of Mammalogists (Sikes et al. 2016) and the guidelines for the treatment of animals in behavioral research (Vitale et al. 2018). All procedures were approved by the National Research Centre for Carnivores Conservation-ICMBio/CENAP, in Brazil (license numbers: SISBIO 30053–1, 30053–4, 30053–5, 30053–7, 30053–8, 61.844–2, 61.844–3, and 61.844–5).

Competing interests The authors declare no competing interests.

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