Journal of Mammalogy, XX(X):1–13, 2023
https://doi.org/10.1093/jmammal/gyac123

Unveiling demographic and mating strategies of *Panthera onca* in the Pantanal, Brazil

Carlos Eduardo Fragoso,[1,*] Lilian Elaine Rampim,[1] Howard Quigley,[2,†] Mario Buhrke Haberfeld,[1,2,3] Wellyngton Ayala Espíndola,[1] Valquíria Cabral Araújo,[1] Leonardo Rodrigues Sartorello,[1] and Joares Adenilson May Júnior[1,2,4]

[1]*Associação Onçafari, Rua Ferreira de Araújo, 153, Conjunto 14, Sala 4, Pinheiros, 05428-000 São Paulo, São Paulo, Brazil*
[2]*Panthera Corporation, 8 West 40th Street 18th Floor, New York, New York 10018, USA*
[3]*Instituto SOS Pantanal, Rua Alberto Neder, 328, Centro, 79002-160 Campo Grande, Mato Grosso do Sul, Brazil*
[4]*Laboratório de Protozoologia e Rickettsioses Vetoriais, Faculdade de Veterinária, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil*

**To whom correspondence should be addressed: edu@oncafari.org*
†In memoriam

We conducted the first long-term and large-scale study of demographic characteristics and reproductive behavior in a wild jaguar (*Panthera onca*) population. Data were collected through a combination of direct observations and camera trapping on a study area that operates both as a cattle ranch and ecotourism destination. Jaguars exhibited two birth peaks: April/May and October/November, that are the end and the beginning of the wet season in the Pantanal, respectively. The average litter size was 1.43 ± 0.65. Single cubs made up a total of 65.7% of the births, and we found a slight predominance of females (1.15:1 ratio) in litters. The mean age at independence was 17.6 ± 0.98 months, with sex-biased dispersal, with all males ($n = 27$) leaving the natal home range and 63.6% of females exhibiting philopatry. The interbirth intervals were 21.8 ± 3.2 months and the mean age at first parturition was 31.8 ± 4.2 months. Our results estimated a lifetime reproductive success for female jaguars of 8.13 cubs. Our observations also indicate that female jaguars can display mating behavior during cub rearing or pregnancy, representing 41.4% of the consorts and copulations recorded. We speculate that this behavior has evolved as a defense against infanticide and physical harm to the female. To our knowledge, this is the first time that such behavior is described for this species. All aggressive interactions between females involved the presence of cubs, following the offspring–defense hypothesis, that lead to territoriality among females in mammals, regardless of food availability. In the face of growing threats to this apex predator, this work unveils several aspects of its natural history, representing a baseline for comparison with future research and providing critical information for population viability analysis and conservation planning in the long term.

Key words: behavior, conservation planning, demography, infanticide, jaguars, Pantanal, population dynamics, reproduction

Este é o primeiro estudo de longo prazo e em grande escala de características demográficas e de comportamento reprodutivo em uma população selvagem de onças-pintadas (*Panthera onca*). Os dados foram coletados por meio de uma combinação de observações diretas e armadilhamentos fotográficos em uma área de estudo que atua tanto como fazenda de pecuária quanto como destino ecoturístico. As onças-pintadas apresentaram dois picos de nascimento: abril/maio e outubro/novembro, que são o final e o início da estação chuvosa no Pantanal, respectivamente. O tamanho médio da ninhada foi 1.43 ± 0.65. Filhotes únicos representaram um total de 65.7% dos nascimentos, e encontramos uma ligeira predominância de fêmeas (proporção 1.15:1) nas ninhadas. A idade média de independência foi de 17.6 ± 0.98 meses, com uma dispersão sexo-assimétrica, com todos os machos ($n = 27$) deixando a área natal e 63.6% das fêmeas apresentando filopatria. O intervalo entre ninhadas foi de 21.8 ± 3.2 meses e a idade média da primeira cria foi de 31.8 ± 4.2 meses. Nossos resultados estimaram um sucesso reprodutivo médio ao longo da vida para onças-pintadas fêmeas de 8.13 filhotes. Nossas observações também indicam que as onças-pintadas fêmeas podem apresentar comportamento de acasalamento durante a criação dos filhotes ou da gestação, representando 41.4% das cortes e cópulas registradas. Especulamos que esse comportamento tenha evoluído como uma defesa contra infanticídio e danos físicos à fêmea. Segundo nosso conhecimento, está é a primeira vez que tal comportamento é descrito para esta espécie. Todas as interações agressivas entre fêmeas envolveram a presença de filhotes, seguindo a hipótese de defesa da prole, que levam à territorialidade entre fêmeas em mamíferos, independentemente da disponibilidade de alimento. Diante das crescentes ameaças a este predador de topo, este trabalho revela vários aspectos de sua história natural, representando uma base de comparação com pesquisas futuras e fornecendo informações críticas para a análise de viabilidade populacional e planejamento de conservação em longo prazo.

Palavras-chave: comportamento, demografia, dinâmica populacional, infanticídio, onça-pintada, Pantanal, plano de conservação, reprodução

Mammals have developed a wide repertoire of reproductive strategies during their evolution, driven by different selective forces (Clutton-Brock 1989). These forces generated behavioral polymorphisms not only among different species, but also intraspecifically in response to variations in social and ecological environment among populations and individuals (Gross 1996).

Promiscuity is one of the most common reproductive systems among mammals, in which males and females copulate with different mates without a continuous bond between the pair after copulation (Clutton-Brock 1989). Despite the substantial costs that this strategy can cause for females, since fertilization can be provided by a single male, promiscuity can play an important role in minimizing inbreeding in populations facing severe genetic bottlenecks (Michalczyk et al. 2011).

Infanticide perpetrated by males is one of the most discussed selective forces for the evolution of promiscuity in females. Altmann et al. (1978) consider infants as the “perfect contraceptives,” leading to the evolution of infanticide and thus counterstrategies to protect offspring, such as aggressivity and multi-male mating. Promiscuity in females occurs in at least 133 species of mammals (Wolff and MacDonald 2004), and such strategy would confuse paternity (paternity uncertainty hypothesis; Hausfater and Hrdy 1984), providing a plausible explanation for the origin of this behavior in many mammal species. Under this hypothesis, females would mate with any males they are likely to have future encounters with in the presence of dependent young, instead of selecting the highest-ranking partner possible (good genes hypothesis; Bellemain et al. 2006), which could decrease the fitness of offspring (Wolff and Macdonald 2004). Based on this hypothesis, Wolff and MacDonald (2004; 130) consider that despite the costs involved in this counterstrategy for infanticide, females “make the best of a bad job.”

According to the sexual selection hypothesis (Hrdy 1979), the benefits resulting from infanticide for the perpetrator male could include the elimination of the cubs sired by other males, shortening of the victimized interbirth period of a female, and increasing the possibility of the perpetrator siring the subsequent litter. Therefore, females would use nonconceptive matings at appropriate times (e.g., immediate or future protection for the litter). Infanticide has been reported in at least 91 species or subspecies of mammals (Ebensperger 2018). Soares et al. (2006) consider that the order Carnivora is the group most likely to commit infanticide among mammals, and promiscuity is present in 87% of the 40 species of carnivores considered vulnerable to infanticide (Wolff and MacDonald 2004). According to Packer et al. (2009), solitary carnivores are even more susceptible to infanticide than social species, as they do not have a cooperative defense. Among large felids, this behavior has been reported in pumas (*Puma concolor*; Logan and Sweanor 2001), leopards (*Panthera pardus*; Bailey 1993; Balme et al. 2013), tigers (*Panthera tigris*; Goodrich et al. 2008), and lions (*Panthera leo*; Pusey and Packer 1994).

The paternity uncertainty hypothesis has been tested in some species under controlled experiments (McCarthy and Vom Saal 1986), but information is still scarce under natural conditions (Lane et al. 2008). Much of what is available in literature is limited and derived from opportunistic data, because many species are elusive, solitary, nocturnal, and females keep their altricial young in underground dens or secretive nest sites (Packer and Pusey 1983; Wolff and Peterson 1998; Bellemain et al. 2006; Balme and Hunter 2013). Thus, reliable data on this behavior are difficult to obtain in free-living animals.

Given that infanticide is widespread among animals, it may have an important role in regulating mammalian population dynamics and intraspecific interactions, as well as the counterstrategies to avoid it. To better understand how natural populations respond to these forces over time, long-term studies need to be conducted in order to provide reliable information. Long-term studies also facilitate a better comprehension of many other aspects of the biology and ecology of species. This information is often impossible to obtain through specific and short-term studies, even though it is crucial for the conservation of species (Holt et al. 2003). Intense field efforts with direct observations and systematic records, as well as with habituation of individuals to the presence of observers, also increase the accuracy of information, especially in species of more elusive habits. Of the 40 wild cats, only lions (Packer et al. 1988), tigers (Smith and McDougal 1991; Kerley et al. 2003), cheetahs (*Acinonyx jubatus*; Kelly et al. 1998), pumas (Logan and Sweanor 2001), and leopards (Balme et al. 2013) have had their reproductive parameters reliably estimated (Balme et al. 2013). To date, there is no information regarding these estimates in a free wild jaguar (*P. onca*) population.

The jaguar, an apex predator on the American continent, is considered solitary and territorial (Hunter 2019). Jaguars are globally classified as 'Near Threatened' by the IUCN Red List (Quigley et al. 2017) and already have disappeared from more than a half of their original distribution (Paviolo et al. 2016). Their populations are declining rapidly in several regions, being considered threatened in several countries (de la Torre et al. 2017a) due to habitat loss, depletion of the prey base, and human persecution (Paviolo et al. 2016). The home ranges of adult males are generally larger than females and with intense spatiotemporal overlap between the sexes (female jaguars overlapped an average of 64% of their home range with males; Cavalcanti and Gese 2010). Despite being the most studied felid in the neotropical region (Desbiez and Paula 2012), jaguars are considered one of the most difficult big cats to study in the world (Harmsen et al. 2010). Most studies about this species are focused on habitat use, home ranges, activity patterns, and density estimates (Harmsen et al. 2011; Morato et al. 2018). Information on behavioral and reproductive aspects is scarce and generally based on captive animals (Morato et al. 2004; Jorge-Neto et al. 2018) or in specific cases with a maximum of four free-living individuals (Soares et al. 2006; Carrillo et al. 2009; Pinho et al. 2014). Jaguars are considered polyestric with no reproductive season (Leuchtenberger et al. 2009). Considering the importance of this big cat as a key component of several ecosystems (Paviolo et al. 2016), it is important to better understand the mechanisms that affect its dynamics in the wild.

Here we present data from wild jaguars in a systematic long-term study in the Pantanal wetlands of Brazil. Previous studies have estimated a density of 6.5–7.0 individuals per 100 km^2 in the region (Soisalo and Cavalcanti 2006; Azevedo and Murray 2007). We seek to describe reproductive interactions among jaguars, specifically to address for the first time the strategies used by females to minimize the chances of infanticide. We also seek to contribute with demographic information related to mating, births, litter sizes, interbirth intervals, age at independence, dispersal, sexual maturity, and lifetime reproductive success. We tested the hypothesis that observed birth pulses characterized jaguars as seasonal breeders, and if so, whether there is a correlation between rainfall and parturitions. We attempted to identify factors that could motivate intraspecific aggression among individual jaguars. Through our work, we seek to fill several gaps in knowledge about jaguar demography and mating patterns that previously hindered more accurate analyses evaluating its conservation status in Brazil (Desbiez and Paula 2012), a key country to the long-term survival of this species. Many core populations of jaguars do not contain enough individuals to provide for long-term survival; therefore, connectivity between populations is a critical issue (Rabinowitz and Zeller 2010). Many of the demographic parameters described herein are tied to the production of dispersing individuals and thus the potential movement of individuals between populations.

MATERIALS AND METHODS

Study area.—The Pantanal is one of the largest continental wetlands in the world, situated in the upper Paraguay River basin, which encompasses approximately 180,000 km^2 across Brazil (78%), Bolivia (18%), and Paraguay (4%; Tomas et al. 2019). The Pantanal has a well-defined seasonality with a unimodal precipitation distribution, wherein approximately 80% of the total annual precipitation is concentrated between October and March (rainy season), when the water collected in the surrounding highlands gradually flows to the lower sections of the Paraguay River (Tomas et al. 2019; Thielen et al. 2020). Throughout the dry season, water is restricted to permanent rivers and sloughs (Crawshaw and Quigley 1991). According to the Köppen classification system, the climate in the region is Aw (tropical wet with extended winter dry season or savanna climate), with mean daily temperatures of 23.8°C, 70.26% for humidity, and 1,197 mm for mean yearly precipitation (Alvares et al. 2014; de Souza et al. 2018). Approximately 84% of the natural vegetation of the Pantanal is still intact (MapBiomas 2020). The Pantanal harbors one of the largest remaining, contiguous jaguar populations (Soisalo and Cavalcanti 2006; Kantek et al. 2021). Besides jaguars, this floodplain also harbors healthy populations of iconic and threatened species such as hyacinth macaw (*Anodorhynchus hyacinthinus*), giant anteater (*Myrmecophaga tridactyla*), tapir (*Tapirus terrestris*), marsh deer (*Blastocerus dichotomus*), white-lipped peccary (*Tayassu pecari*), and pampas deer (*Ozotoceros bezoarticus*; Tomas et al. 2019). Caiman Ecological Refuge (CER) is approximately 530 km^2 located between the municipalities of Miranda and Aquidauana, in the state of Mato Grosso do Sul, Brazil (19°57′02″S, 56°18′14″W). The CER has been an operating cattle ranch for more than six decades, with a mean herd size of approximately 15,000 head during the study period. The CER also added wildlife tourism to the economic activities in 1987. The ranch is located in a transition zone between the Pantanal and Cerrado biomes (Kanda et al. 2019). The landscape is composed of a mosaic of vegetation types, including: marshlands; exotic pastures such as perennial tropical grass (*Urochloa humidicola*; ~25%) designated for cattle rearing; native pastures where there is no cattle ranching activity (~49%), comprising native grasses such as *Andropogon bicornis*, *Anoxopus purpusii*, and *Elionurus muticus*, and the common presence of sandpaper trees (*Curatella americana*); semideciduous forests (~18%); and patches of many different sizes of forest vegetation in a matrix of savannah grasslands with significant presence of trumpet trees (*Handroanthus heptaphyllus* and *Tabebuia aurea*), tarumãs (*Vitex cimosa*), fig trees (*Ficus* sp.), and acuri palm trees (*Attalea phalerata*; ~6%), with canopy reaching 10–20 m tall (Crawshaw and Quigley 1991). Approximately 56 km^2 is set aside as legally designated private forest reserve. Much of the area is flat at a mean elevation of 110 m above sea level and floods during the rainy season. Approximately 88–120 people live on the ranch, fluctuating from a low in the wet season to a high in the dry season. There are approximately 83.6 km of roads and many man-made waterholes for cattle (*Bos taurus*) and wild animals spread across the ranch. Research on jaguars on the study area began in 2011 in parallel to the habituation process of this species to free-living observations and ecotourism.

Data collection.—From 2011 through early 2020, all jaguars recorded through direct observation or camera trap were named and an identification guide was created, with pictures of the face, right and left side, and different angles of the rear of each individual, which was used to compare the records and identify them to individual level according to their unique coat patterns (rosettes). This identification guide is updated regularly with better pictures or with the addition of new individuals. It contains more than 180 different jaguars recorded over the study period and each has its own detection history, with gathered information through sightings reports, camera-traps records, and GPS locations (detailed below)——allowing us to have long-term demographic monitoring for the local population. Data on social structure, reproductive behavior, and demography of jaguars were collected using the following four methods.

One: camera trapping.—Each year, from 2012 through 2019, 15–77 camera traps (Bushnell, Overland Park, Kansas) were distributed on known trails most used by jaguars (according to tracks, sightings, and GPS locations) on the study area, without following any grid sampling design. Cameras were set to record video, with a recording time of 30 s and an interval of 1 s between recordings. Each camera was visited monthly to download the recorded videos, change batteries, and assure proper functioning of the camera. All videos were stored in the project database and all wildlife were identified manually to species; all jaguars were identified by team members to individual level using their unique spot patterns and the identification guide to jaguars of the study area; a unique identifier was provided for each record to provide for verification.

Two: GPS monitoring and radiotelemetry.—Jaguar captures were undertaken three to four times per year by an experienced team, each trapping period lasting 2 weeks. Captures were performed through the use of Aldridge spring-activated foot snares (de la Torre et al. 2017b) set on known trails used more frequently for the target individuals or around carcasses, usually cattle (killed or just consumed opportunistically by jaguars). Jaguars were anesthetized with a combination of tiletamine–zolazepam intramuscularly by CO_2 rifle dart (Onuma et al. 2015; May-Junior et al. 2021). Capture procedures were approved by National Research Center for Carnivores Conservation——ICMBio/CENAP under license numbers No. SISBIO 30.053, 52.734, and 61.844, and followed the guidelines of American Society of Mammalogists (Sikes et al. 2016). Jaguars were identified to individual and aged according to their detection histories (if followed since cubs) or teeth and body size/condition (presence of scars, tooth wear). Each captured adult jaguar older than 2 years was fitted with a radio collar (Lotek Wireless, New Market, Ontario, Canada; Sirtrack Ltd., Havelock North, New Zealand; Telonics Inc., Mesa, Arizona) before being released back into the study area. Collars were programmed to seek 24 locations per day through GPS uplink; periodically, collared animals were also located from the ground through the VHF signal that was also emitted from the collar, at which time jaguars were tracked subsequently through direct observation.

Three: active searches.—Tracks and visiting areas known to be used intensively by jaguars were followed on a daily basis by the field team (researchers/biologists and local nature guides). Observations by guests of the lodges, who are taken by two experienced guides (one from the local community and one bilingual guide) to game drives in the morning (05:30 to 11:00 h) and in the afternoon (15:00 to 18:00 h) to observe and count wildlife, were incorporated. Night-time searches (19:00 to 21:00 h) were performed regularly using a strong spotlight from the back of an open-bed vehicle while driving slowly on roads in the study area. Since the habituation technique was first implemented at CER in 2011, the sighting rate of jaguars increased from 138 to 905 per year over the study period, and the animals became habituated to human presence. The habituation process was developed through intensive monitoring and without baiting or domestication. Animals were accompanied by observers (researchers, guides, lodge guests, and lodge staff) from vehicles at a distance in order not to interfere with their natural behavior. Being a charismatic species and the largest predator in the Americas, the jaguar is the most targeted animal for tourism in the Pantanal. The field team and guides maintain frequent radio contact with each other to maximize the opportunity of locating such species. During the high season of tourism at CER (late May to late November), there are an average of seven safari or monitoring vehicles in the field, a number that drops to four vehicles in the low season (early December to early May). Guides and researchers became familiar with many jaguars, but the sightings are confirmed with photo ID of the individuals through their spot patterns.

Four: opportunistic encounters.—During the normal course of ranch staff activities in the study area, encounters with jaguars were reported to project team members. Identification of jaguars was made during these encounters or through the use of photographs.

For the combined overall database on jaguars, behavioral descriptions were converted into binary data on the presence/absence of selected variables, such as presence of GPS/VHF collar, presence of young, consorts, presence of additional adult jaguars, observed copulation, aggressive behavior, and presence of carcass; along with details of the observations including date, time, duration, sex, estimated age of young, coordinates, site, and identification of individuals. Unlike lions, jaguars do not vocalize during their daily prowls, but when in heat, female jaguars become vocal and very active. When found by a mate, females start to rub on objects (e.g., shrubs, trunks, grass), roll on their back, and vocalize intermittently. We considered consort when the male was following a female and she responded with vocalizations, rubbing, and rolling behaviors. Copulation was assumed when a male mounted the female, making thrust movements, usually followed by a nape bite, vocalization of both jaguars (growl and roar), and the female rolling into lateral dorsal decubitus (for a more detailed description of mating behaviors, see Jorge-Neto et al. 2018). When copulation was not observed, it was possible to determine when it occurred by listening to characteristic copulatory roars. Aggressive behaviors were considered when an attack followed by a fight (with physical contact) occurred between jaguars (see in more details in Stanton et al. 2015). The same process was carried out with the images of the camera traps. Where interactions between adult males and females occurred, data were compiled using freely available Timelapse Image Analysis System (Greenberg and Godin 2015). Respective metadata with date and time of the records were exported to spreadsheets, where complementary information was inserted, such as geographic coordinates, animal identification, presence of radio collar, observed mating behavior, presence of cubs and duration of recording.

Birth dating, litter size, and gender determination.—Through the field monitoring of females equipped with GPS/VHF collars, we were able to define dates of parturition within a day or two by observing when clusters of points commenced in one place, later being examined for the presence of cubs when possible. Dens were approached on foot by two team members avoiding disturbance and mischaracterization of the den site while the mother jaguar was being tracked at a minimum distance of 300 m by other team members, communicating through two-way radios. Cubs observed with females without radio collars were provided with an estimated age based on comparisons with cubs of known age and the proportion of body size in relation to their mothers. Considering a minimum period of 93 days gestation for the species (Hunter 2019), the approximate date of birth of the cubs was estimated. Litter size was defined as the number of individuals accompanying a female or identified in a den. We identified the sex of each cub when possible. Cubs that disappeared were assumed to have died. From 56 litters in total, those cubs first observed at estimated age of older than 6 months were excluded from parturition data analysis to increase accuracy. We used Chi-square analysis to evaluate the seasonality of births throughout the months (Supplementary Data SD1).

Rainfall data.—We collected data daily in the morning using a conventional rain gauge and entered manually into our on-site database. We used the Pearson's correlation test in R language (T. R. Core 2019) to evaluate the correlation between rainfall data and the months when the cubs were born.

Age at independence and dispersal.—For young jaguars with at least one monthly observation record, the dates of the last continuous records with and without the respective mothers were noted, defining the period in which they became independent. Only cubs observed for the first time with an estimated age of less than 6 months were considered to increase accuracy. We assumed that young jaguars no longer associated with their mothers have become independent and animals that disappeared from the study area after 18 months were assumed to have dispersed (age at independence estimated by Crawshaw and Quigley 1984). Records of the individuals in the study area were also noted to indicate whether they dispersed or remained in areas adjacent to their mothers. As young first-dispersing jaguars are not fully grown when they reach independence, the team never placed GPS/VHF collars on individuals at this age to track them while dispersing.

Interbirth intervals.—We calculated the average interval between successful litters, where at least one cub reached independence and dispersed from the mother, as well as the interval between unsuccessful litters.

First parturition and lifetime reproductive success.—For each female followed from an early age, with an accurate age estimate, the time of first observed copulation and confirmed pregnancy was defined, establishing the age of first reproduction of the study population. Using the interbirth interval (ii), mean litter size (ls), age at first (fp), and age at last parturition (lp), we estimated the lifetime reproductive success (lrs) as:

$$lrs = ls\left(\frac{lp - fp}{ii}\right)$$

Female–male interactions, consorts, and matings.—Mating encounters (consorts and copulations) were obtained through camera traps and direct observations. Camera-trap documentation of matings was relatively rare ($n = 4$) and was simply due to the choice of location by an animal, by chance in front of an established camera site. After mating was documented, subsequent records for the same female pairing with the same/different male during the following 7 days (maximum pairing period registered in this study) were not used in the analysis, lacking independence between records. To assess the annual cycle of consorts and matings, females and males with at least one monthly record were selected for analysis.

Intraspecific aggression.—Aggressive interactions between individuals of the same sex were compiled and described with accompanying information on the identified individual and the presence of young, prey carcass, or other potentially influencing covariates to allow for analysis resource competition among females and the influence of defending offspring.

Results

Births and litter sizes.—From 38 litters of 21 different females considered in this analysis, 34.2% of the litters were born between April and May ($n = 13$) and 28.9% between October and November ($n = 11$; Fig. 1), although the results show that jaguars cannot be considered as seasonal breeders ($x^2 = 18$, d.f. = 4, $P = 0.2627$). There was no correlation between rainfall and birth of cubs ($P = 0.867$, correlation coefficient = –0.05). The average litter size was 1.43 ± 0.65 ($n = 35$, range = 1–3). In three cases, the females with confirmed pregnancy through visual records and clusters from GPS collars lost the cubs before detection and counting. In one case a litter of triplets were found through the locations of the GPS collar within 5 days after birth and another 'den' was visually verified 56 days after birth. A female tracked by GPS collar was found dead after an intraspecific encounter and two cubs in the final third of gestation were collected during the necropsy. Of 35 litters with recorded and counted cubs, 65.7% were of a single cub, 25.7% were twins, and 8.6% were triplets. There was a slight predominance of females (1.15:1 ratio, $n = 50$) in the registered litters.

Age at independence and dispersal.—The mean age at independence was 17.6 ± 0.98 months ($n = 18$ litters, range = 17–21). Of the 27 males that were born in the study area and reached independence, only two were registered in the following years, although they did not remain more than 13 months after dispersal, leaving the area again. For 33 females born at CER, 21 remained in the adjacent area of their mother after independence.

Interbirth intervals.—The interval between successful litters ($n = 10$) was 21.8 ± 3.2 months (range = 17–27 months). Among unsuccessful litters ($n = 4$) the interval was 9.5 ± 4 months (range = 6–15 months).

First parturition and lifetime reproductive success.—A mean age at first parturition for female jaguars in this study was 31.8 ± 4.2 months ($n = 6$, range = 25–37). A female had her first litter at 25 months of age. Considering a gestation period of 93–111 days for jaguars (Hunter 2019), conception occurred at around 22 months of age for this particular individual. In four cases, primiparous females lost their litters. However, females still dependent on the mother have been documented mating at 15 months of age. For males, the youngest to mate in the study area was 19 months old.

The oldest female registered in the study area was captured in 2005 by another team and was already an adult, with its birth conservatively estimated according to her body size, tooth wear, gingival recession, and abdominal sagging in 2002. Her last record was in June 2018, which made her at least 16 years old. Another female that was continuously monitored by the project had her last successful offspring at the age of 13 and was found dead of unknown causes at the age of 15 years.

Considering that a female can have her first litter at 2.65 years old and her last litter at 13 years old, a mean litter size of 1.43 cubs and interbirth interval of 1.82 years (Table 1), a female jaguar could generate 8.13 cubs throughout her lifetime.

Female–male interactions, consorts, and matings.—Between 2013 and 2019, 493 interactions between males and females were documented (excluding interactions between mothers and their offspring), totaling 14,817 min of direct field observations ($n = 313$) and 90 min of video recorded by camera traps ($n = 180$). Consorts occurred on 381 and copulations on 108 occasions, totaling 113 and 65 independent interactions, respectively, between 17 females and 17 different males (Fig. 2).

In 37 of 108 observed matings, the time of each copulation was recorded ($n = 202$), generating 4,298 min of observations. Copulations (mount to dismount) had a minimum duration of 5.3 s, a maximum duration of 112 s, and a minimum time of 1

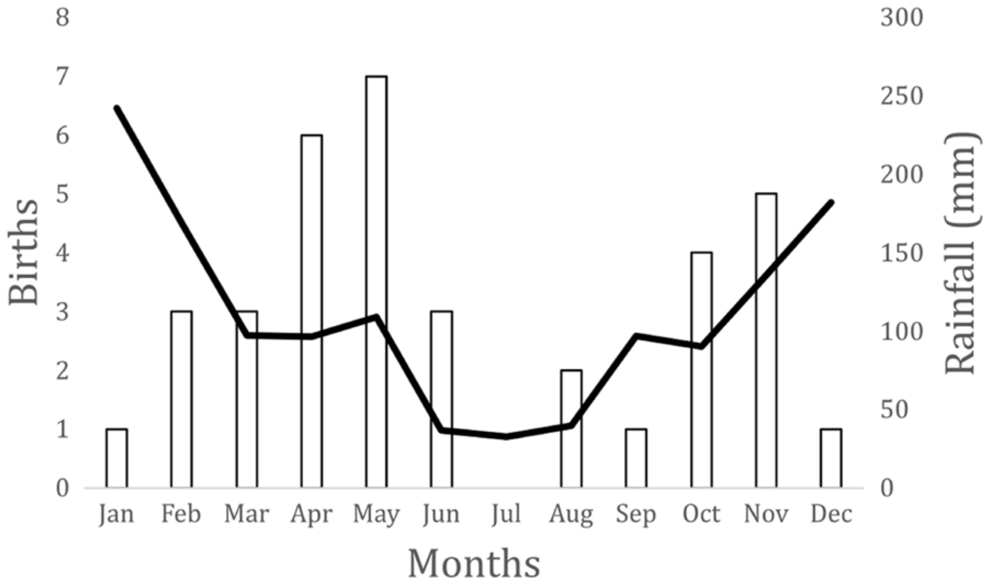

Fig. 1.—Births of jaguar cubs (*Panthera onca*) compared to average rainfall at Caiman Ecological Refuge, Miranda, Brazil, from 2009 to 2019 (line = rainfall and bars = births per month).

Table 1.—Reproductive parameters estimated by this study to calculate the lifetime reproductive success of female jaguars (*Panthera onca*) at Caiman Ecological Refuge, Miranda, Brazil, from 2011 to 2019.

Parameter	*n*	Mean	Median	*SE*	*SD*	Min	Max
Litter size (cubs)	35	1.43	1	0,11	0,65	1	3
Age at independence[a]	18	17.6	17	0,23	0,98	17	21
Interbirth interval between successful litters[a]	10	21.8	21.5	1,01	3,20	17	27
Interbirth interval between unsuccessful litters[a]	4	9.5	8.5	2,00	4,00	6	15
Age at first parturition[a] (Supplementary Data SD1[/scolor])	6	31.8	32	1,71	4,20	25	37

n = sample size; *SE* = standard error; *SD* = standard deviation; min = minimum estimate; max = maximum estimate.

[a] Months.

m between each. Copulations occurred at any time of the day but were mainly concentrated in the early morning and after 16:00 h (Fig. 3). Therefore, ambient temperature may be a factor in determining copulations in jaguars. Often, during the hottest hours of the day, couples were observed resting in separate places, meeting each other again when the temperature was milder. During mating periods, jaguars did not hunt, eating opportunistically when they found a carcass (sometimes steeling it from another jaguar).

Conceptive and nonconceptive matings.—In 14 of the 113 independent mating events (consorts and/or copulations) recorded, it was not possible to define whether the female was pregnant due to the lack of subsequent observations. In the remaining 99 events, 41.4% of the females were pregnant or with dependent offspring (10 days to 14 months of age), and in 58.6% they were without dependent young and possibly receptive to fertilization, hereafter called conceptive and nonconceptive matings, respectively. They stayed paired with males over

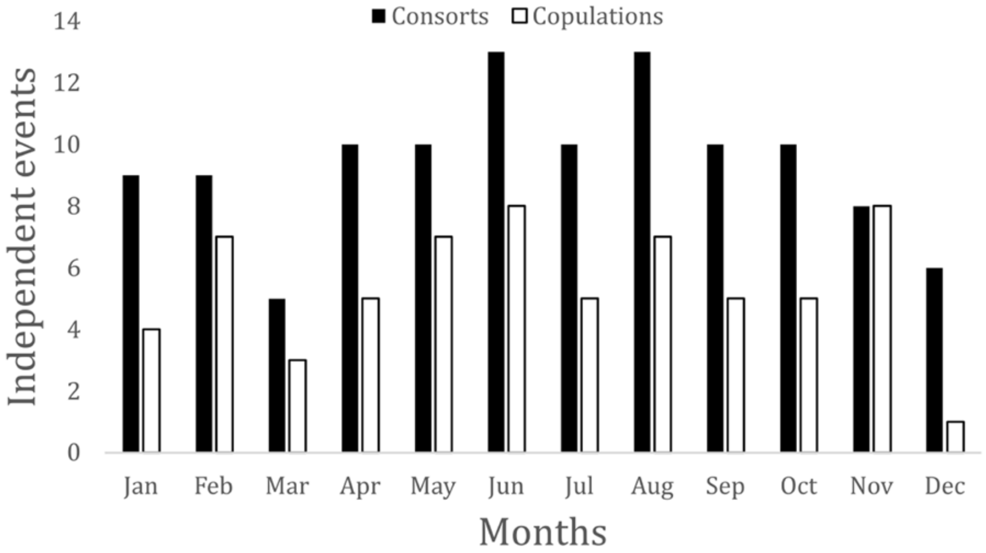

Fig. 2.—Monthly distribution of independent mating periods (n = 65) of jaguars (*Panthera onca*) at rainfall at Caiman Ecological Refuge, Miranda, Brazil, from 2013 to 2019.

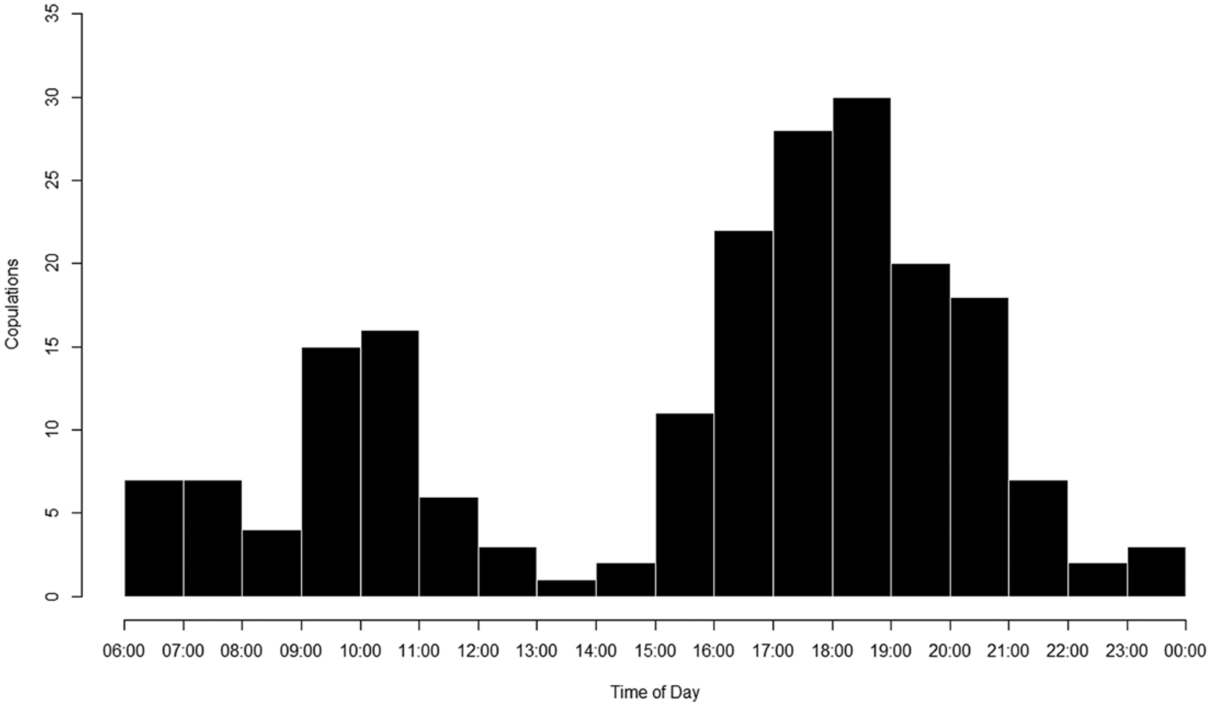

Fig. 3.—Distribution of jaguar (*Panthera onca*) copulations by the hours of the day (the intervals between 00:00 and 05:59 were excluded due to the absence of field observers) observed at Caiman Ecological Refuge, Miranda, Brazil, from 2016 to 2019.

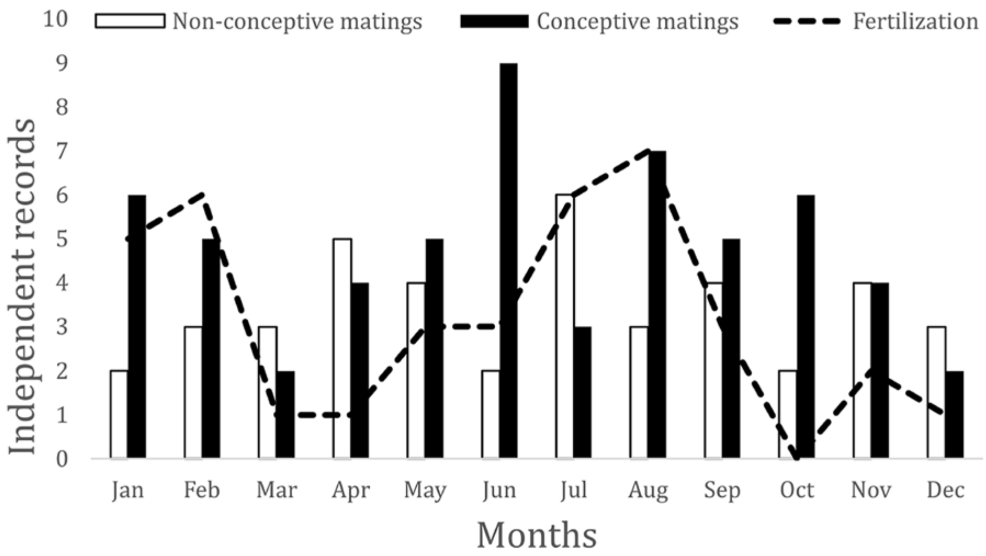

Fig. 4.—Comparisons between fertilizations, conceptive, and nonconceptive matings by *Panthera onca* throughout the months at Caiman Ecological Refuge, Miranda, Brazil, from 2013 to 2019.

an average period of 1.6 (range = 1–5) and 2.1 days (range = 1–7), respectively. Considering a minimum gestation period of 93 days, we estimated the periods in which the conceptions of the cubs occurred, in search of a correlation between them and the conceptive matings. There was a positive correlation between the months of fertilization and mating without the presence of offspring or pregnancies ($P = 0.038$, correlation coefficient = 0.131). Intensive mating periods were accompanied by peaks of conception, indicating that these interactions resulted in high chances of fertilization (Fig. 4).

Physical aggression.—In 100% of the 16 aggressive interactions recorded among females, at least one of the females was accompanied by dependent offspring. However, in 75% of aggressive female–female interactions there were medium and large carcasses involved, such as cattle, capybara (*Hydrochoerus hydrochaeris*), and feral hog (*Sus scrofa*). For aggressiveness between males, in all the interactions ($n = 4$) there was a female displaying mating behaviors.

Discussion

Births and litter sizes.—Jaguars in our study area appear to have two peak periods for births that correspond to the end and the beginning of the wet season, respectively. In the llanos of Venezuela, a region with a similar seasonal flooding regime to the Pantanal, peaks of birth were recorded in the dry season, between December and March (Hoogesteijn and Mondolfi 1992). During lactation, some females were observed up to 3 days away from the cubs. The flood risk to dens may be high during the rainy season (January to March). In this period there is a reduction in the availability of dry areas, which can result in an increased rate of encounters between conspecifics (Crawshaw and Quigley 1984), which may expose the young to infanticide or even to predation by other species. There is likely also to be an advantage to pre-dry-season birth pulse in that waters are receding, primary productivity is on the rise, and this normally correlates with the production of herbivores, such as capybaras (Alho et al. 2011), and a higher availability of caimans (Campos and Mourão 2020), the two main wild prey in the study area, thus creating more easily accessible prey for the mother. The average litter size in this study (1.43 ± 0.65) was lower than the average for other big cat species (Table 2). We also found a predominance of single cubs, different from another study of 23 littlers in Belize, in which percentages were 35% single cubs, 52% twins, and 13% triplets (Rabinowitz 1986). Detection of the number of cubs per litter often occurred at approximately 3 months of age, so the actual litter size may be underestimated due to early mortality. In pumas, for example, 65% of the mortality of cubs occurred when they were ≤3 months old (Logan and Sweanor 2001). For Siberian tigers, the average litter size was 2.4 ± 0.6, but dropped to 1.3 ± 0.5 after considering the mortality rate after 12 months of life (Kerley et al. 2003).

Age at independence and dispersal.—Our results corroborate the data previously offered by Crawshaw and Quigley (1984). The mean of 17.6 months is about average for most big cat species (Hunter 2019), although examples can be at much younger ages, such as for pumas, 13.7 ± 1.6 months (Logan and Sweanor 2001; for comparison with other big cats, see Table 2). Sporadic encounters between mothers and cubs occurred after independence, mainly at large carcasses (e.g., cattle), and primarily by the mother and her female offspring. However, when the mother already had a new litter, agonistic behaviors occurred from the mother to the older cubs, probably by considering them a threat for the younger ones.

According to our analyses, there is a sex-biased dispersal in jaguars, with females being predominately philopatric and males performing dispersal outside of their natal home range, as suggested by other studies (Crawshaw and Quigley 1991; Bernal-Escobar et al. 2015; Kantek et al. 2021). This male-biased

Table 2.—Reproductive parameters estimated by this study (*Panthera onca*) at Caiman Ecological Refuge, Miranda, Brazil, from 2011 to 2019, in comparison with other big cat species: leopard (*Panthera pardus*), tiger (*Panthera tigris*), lion (*Panthera leo*), puma (*Puma concolor*), and cheetah (*Acinonyx jubatus*).

Parameter	Jaguar	Leopard	Tiger	Lion	Puma	Cheetah
Litter size	1.43 ± 0.65 ($n = 35$)	1.9 ± 0.1 ($n = 140$)	2.4 ± 0.6 ($n = 16$)	2.3 ± 0.9 ($n = 34$)	2.2 ± 0.8 ($n = 21$)	2.1 ± 1.0 ($n = 105$)[a]
Age at independence	17.6 ± 0.98 ($n = 18$)	19 ± 1 ($n = 52$)	18.8 ± 1.5 ($n = 5$)	30[b]	13.7 ± 1.6 ($n = 12$)	17.1 ± 1.9 ($n = 70$)
Interval between successful litters	21.8 ± 3.2 ($n = 10$)	25 ± 1 ($n = 55$)	21.4 ± 4.4 ($n = 7$)	22.1 ± 4.1 ($n = 7$)	17.4 ± 2.5 ($n = 16$)	20.1 ± 3.0 ($n = 36$)
Interval between unsuccessful litters	9.5 ± 4 ($n = 4$)	11 ± 1 ($n = 46$)	7 ($n = 1$)	9.3 ± 4.3 ($n = 13$)	—	—
Age at first parturition	31.8 ± 4.2 ($n = 6$)	46 ± 2 ($n = 26$)	48.0 ± 4.8 ($n = 4$)	46.5 ± 11 ($n = 10$)	29.1 ± 6.0 ($n = 12$)	28.8 ± 3.1 ($n = 22$)
Reference	This study	Balme et al. (2013)	Kerley et al. (2003)	Schaller (1972)	Logan and Sweanor (2001)	Kelly et al. (1998)

[a] Litter size at independence.

[b] Limited data provided by the author.

dispersal may have evolved as a mechanism of inbreeding avoidance, as male jaguars do not establish their territories close to females that they are related to, decreasing the chances of inbreed mating that would reduce the genetic variability of the population. Future studies in lower density populations are needed to evaluate if this mechanism occurs across the range of the species.

Interbirth intervals.—The interval between successful litters in our study area was slightly lower than the 22–24 months observed by Carrillo et al. (2009) for jaguars in Costa Rica, but is similar to tigers (Kerley et al. 2003) and cheetahs (Kelly et al. 1998), but higher the 17.4-month interval for pumas (Logan and Sweanor 2001; Table 2). Among unsuccessful litters, we found lower ages compared with the 11 ± 1 months ($n = 46$, range = 4–36) observed for leopards (Balme et al. 2013). We never recorded females rearing two consecutive litters simultaneously, but a few weeks prior to dispersal of the cubs they can get pregnant again, as documented by this study.

First parturition and lifetime reproductive success.—This study revealed a precocity of female jaguars regarding first parturition if compared with other big cats (Table 2). The wide variance in our data may be due to failures to detect parturition quickly or may be related to social aspects, such as variation in the establishment of a favorable territory for the raising of cubs, or even physiological differences among individuals (Balme et al. 2013). The youngest female jaguar to give birth for the first time was 25 months old, younger than the 36–42 months suggested by Hunter (2019) but corroborates the information from Seymour (1989) and Sunquist and Sunquist (2002). Considering a gestation period of 93–111 days for jaguars (Hunter 2019), conception occurred at around 22 months of age for this particular individual. We recorded dependent female cubs copulating with males at 15 months of age, younger than the 24–30 months suggested by Hoogesteijn and Mondolfi (1992)—earlier than South African leopards that were observed mating for the first time at 35 ± 3 months (Balme et al. 2013). According to our results, males mated for the first time earlier than the 36–48 months suggested by Crawshaw and Quigley (1984). The precocity of female jaguars in establishing residency shows that they are able to successfully ensure resources needed to raise cubs earlier than other big cats, which may be related to prey abundance in the study area, and thereby extending their reproductive age.

A maximum life span found in this study was at least 16 years old, as suggested by Hunter (2019), and older than the maximum-aged jaguar in Belize of 14 years (Harmsen et al. 2017).

Regarding lifetime reproductive success, the present study shows that a female jaguar could generate 8.13 cubs throughout her lifetime, slightly lower than the 8.6 cubs estimated by Crawshaw and Quigley (1984) who considered a reproductive age between 3.5 and 15 years, with an average litter of 1.5 cubs.

Conceptive and nonconceptive matings.—The results presented in this study call into question the influences and motivations for mating behavior that does not produce young in jaguars. The reasons that motivate female jaguars to mate without reproduction purposes can be considered a counterstrategy to create uncertainty about the paternity of litters and thus minimize the chances of infanticide by conspecific males (Hrdy 1979; Wolff and MacDonald 2004). In addition, jaguars meet the criteria of species vulnerable to infanticide, with altricial nonmobile young and extended parental care (Wolff and MacDonald 2004). Cub remains have been found in the stomach contents of hunted male jaguars in Venezuela (Hoogesteijn and Mondolfi 1992), suggesting that infanticide can be committed by males of this species, with an additional nutritional advantage resulting from cannibalism (Balme and Hunter 2013). For this counterstrategy to have a greater chance of success, it would be necessary for males to have a high capacity for recognizing females with which they previously mated and a low capacity for recognizing paternity. But this low recognition of paternity can have the opposite effect, as observed by Soares et al. (2006), who reported a case in which a male killed his own offspring. Recognition of either mating females or their offspring might become more difficult in a high-density population such as the one we studied.

According to our field observations, camera trap records, and GPS monitoring, the auditory, olfactory, and/or visual auditory stimuli of a male that may represent a risk to the offspring apparently triggers a facultative anovulatory behavior in female jaguars. Among big cats, pseudo-estrus has been reported for lions (Schaller 1972; Packer and Pusey 1983) and pumas (Logan and Sweanor 2001; Benson et al. 2012). Our data showed females with dependent cubs guided males to areas away from locations of offspring to copulate. Benson et al. (2012) observed the same behavior in pumas, where females spend consecutive days mating with males, but return to the den after this period and continue to raise the kittens normally. At the same time that this behavior creates an immediate protection in relation to a possible aggressor, it may confuse paternity. However, when females are away from the cubs during mating, this strategy can expose the litter to predation or infanticide by other individuals, including other females, as well as leaving cubs malnourished.

Another hypothesis that could have a secondary role in nonconceptive matings would be to reduce the availability of sperm to other females, decreasing the chances of conception and intraspecific competition in the future (Sommer et al. 1992; Doran-Sheehy et al. 2009). Situations in which two females (where at least one had a dependent offspring) were competing for the same male have already been registered in the study area, which could corroborate this idea. There is no doubt that mating plays an important role in the complex social lives and dynamics of jaguars.

Our data show that jaguars are promiscuous in the wild, with females adopting a multi-male mating system, probably imparting a level of fitness in their litters and their lifetime contribution of young and successful breeders, but there is evidence that nonestrous mating occurs at levels not previously recorded for the species. We speculate that this strategy developed as a 'best practice' for: (1) reducing the chance of injury or even death for the female; and (2) providing a level of protection for cubs against infanticide. Because female jaguars are smaller than males (by 36.5% difference in mean weight in our study), it would be difficult to ward off a male aggressor. Thus, false mating might not only distract the male, but also create a false bond with the cubs as potentially related to the male; either or both would protect the offspring of the female. We also speculate that even females without dependent cubs and signs of pregnancy can display mating behavior to minimize the chances of infanticide in the future and/or increase their acceptance within the territories of males, which could provide additional protection in future encounters. Promiscuity in other big cat species has also been documented in cheetahs (Gottelli et al. 2007), lions (Packer and Pusey 1983), leopards (Balme et al. 2013), and pumas (Logan and Sweanor 2001). Logan and Sweanor (2001) noted that it is likely that females that mate with as many males as possible will have greater reproductive success throughout their lifetimes. Female jaguars displayed mating behaviors with an average of six different males (*n* = 17, range = 1–11). This strategy could also increase the genetic diversity of the offspring, considering that 34.3% of the litters registered in the study area were multiples (twins or triplets). Several previous studies do not support this hypothesis (Soares et al. 2006; Pinho et al. 2014), but it is known that multiple paternities in the same litter occur in lions (Lyke et al. 2013) and it is possible that it occurs in jaguars, which could be evaluated through genetic studies. With regard to conceptive matings, although promiscuity brings potential benefits to females (e.g., increased fitness of young, protection of the litters), they may also be mating with males of inferior genotypic and phenotypic characteristics to those suggested by mate choice theory (Bellemain et al. 2006). But it is possible that there are other mechanisms that act in a "selection of paternity," such as the duration of the mating period, the number of copulations, and the stimulation caused by each male (Larivière and Ferguson 2003). However, in jaguars, data collected so far have not confirmed that males or females recognize the true paternity of the offspring, as suggested in pumas (Benson et al. 2012). To avoid the risks of infanticide, female jaguars could also adjust counterstrategies, such as parental care. Male jaguars do not participate in the rearing of cubs, so they cannot prevent conspecifics from killing offspring except through territorial exclusion. Alternatively, from what little we know, females remain with their newborn cubs in protected sites for several days, with short excursions. Even so, these places end up concentrating odors and other signs that can attract predators or infanticides. Cubs start to eat solid food and visit the carcasses accompanied by the mother aged approximately 75–90 days (Soares et al. 2006), when the first records of cubs generally occurred, so cub loss may be higher than the one observed by our study.

None of the causes of cub mortality in this study have been identified, but studies in another area of the Pantanal (Tortato et al. 2016) and in the Cerrado (Soares et al. 2006) indicate that infanticide may have an important role in cub mortality. However, it is not yet known how much infanticide, even if common, effects their survival.

Physical aggressions also are an important defense to protect offspring, although this intraspecific behavior is relatively rare in jaguars, as demonstrated by our findings. The only four physical aggressive interactions recorded between males occurred during the courtship of females that displayed signs of estrus (i.e., calling, physical pursuit of the male, physical contact other than mating initiated by the female), offering direct evidence that males compete for females and mating opportunities. In 100% of the 16 aggressive interactions recorded among females, at least one of the females was accompanied by dependent offspring. Wolff and Peterson (1998) propose the offspring–defense hypothesis, in which the threat of infanticide by conspecific females is one of the factors that lead to territoriality among females in mammals, regardless of food availability. However, in 75% of aggressive female–female interactions there were medium and large carcasses involved. As suggested by Tortato et al. (2016), larger prey can attract conspecifics to a site, increasing the chances of antagonistic interactions. These data are not conclusive about the real reason for aggression, whether it would be for food protection, protection of the young, or a combination of both.

Our methods were not intentionally designed to collect data on the reproductive aspects of jaguars, but our long-term monitoring through a combination of methods allowed us to gather relevant information on social, reproductive behavior, and demography of this species. Additional studies specifically focused on these topics will provide more insights into jaguar population dynamics and behavioral aspects across their range as they are influenced by population density, prey availability, habitat quality, and intrinsic behaviors. Anthropogenic factors, such as poaching and persecution, also need to be considered in further studies, since our study area does not have such disturbances and we could not evaluate their effects.

An important consideration for these data and the value of the analysis is their utility in jaguar conservation applications. There has not been a previous in-depth study of jaguar demography in the wild, while many other large felid species——and even more broadly, large carnivore species——have demographic vital signs that are well-described. In fact, often, when there has been a need for demographic modeling for jaguars, puma demographic details were used, such as for the Jaguar Recovery Plan for the United States (USFWS 2018). The Jaguar Corridor (Rabinowitz and Zeller 2010) was developed as a range-wide conservation construct of 58 expert-identified core populations and 65 biological corridors that connect them (Panthera 2018), and is also being institutionalized and endorsed in jaguar range states through the Jaguar 2030 Roadmap for Conservation (UNDP 2021). However, the model still lacks the foundational demographic data for predicting, measuring, and monitoring metapopulation function. The data herein will advance a critical foundation for the range-wide conservation plan for jaguars.

ACKNOWLEDGMENTS

Authors dedicate this article to Dr. Howard Quigley, our mentor, inspiration, friend, and coauthor of this work, who contributed so much to the conservation of jaguars around the world and passed away during the preparation of this study. We thank Caiman Ecological Refuge for allowing such a long-term study. We are also grateful to Bank of America, Log Nature, and Bushnell Corporation for all the support and equipment used in this study. Special thanks to Onçafari (https://oncafari.org/) and Caiman Ecological Refuge (https://caiman.com.br/) members for helping us in collecting the data. We also thank Henrique Villas Boas Concone for reviewing this study.

CONFLICT OF INTEREST

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Combined overall database on births, litter sizes, and age at independence of jaguars (*Panthera onca*) with information from sightings, camera traps, and GPS collars.

LITERATURE CITED

Alho C.J.R., Camargo G., Fischer E. 2011. Terrestrial and aquatic mammals of the Pantanal. Brazilian Journal of Biology 71:297–310.

Altmann J., Altmann S.A., Hausfater G. 1978. Primate infant's effects on mother's future reproduction. Science 201:1028–1030.

Alvares C.A., Stape J.L., Sentelhas P.C., de Gonçalves J.L.M., Sparovek G. 2014. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22:711–728.

Azevedo F.C.C., Murray D.L. 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. Biological Conservation 137:391–402.

Bailey T.N. 1993. The African leopard: ecology and behavior of a solitary felid. Columbia University Press, Ithaca, New York, USA.

Balme G.A., Batchelor A., de Woronin Britz N., Seymour G., Grover M., Hes L., Macdonald D.W., Hunter L.T.B. 2013. Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. Mammal Review 43:221–237.

Balme G.A., Hunter L.T.B. 2013. Why leopards commit infanticide. Animal Behaviour 86:791–799.

Bellemain E., Zedrosser A., Manel S., Waits L.P., Taberlet P., Swenson J.E. 2006. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. Proceedings of the Royal Society of London, B: Biological Sciences 273:283–291.

Benson J.F., Lotz M.A., Land E.D., Onorato D.P. 2012. Evolutionary and practical implications of pseudo-estrus behavior in Florida panthers (*Puma concolor coryi*). Southeastern Naturalist 11:149–154.

Bernal-Escobar A., Payan E., Cordovez J.M. 2015. Sex dependent spatially explicit stochastic dispersal modeling as a framework for the study of jaguar conservation and management in South America. Ecological Modelling 299:40–50.

Campos Z., Mourão G. 2020. Como o jacaré-do-pantanal, *Caiman yacare*, resiste a períodos secos na região central do Pantanal. Embrapa Pantanal, Corumbá, Mato Gosso do Sul, Brazil.

Carrillo E., Saenz J., Fuller T. 2009. Interbirth interval of a free-ranging jaguar. Mammalian Biology 74:319–320.

Cavalcanti S.M.C., Gese E.M. 2010. Spatial ecology and social interactions of jaguars (*Panthera onca*) in the Southern Pantanal, Brazil. Journal of Mammalogy 91:722–736.

Clutton-Brock T.H. 1989. Mammalian mating systems. Proceedings of the Royal Society of London, B: Biological Sciences 126:339–372.

Crawshaw P., Quigley H. 1984. A ecologia do jaguar ou onça-pintada no Pantanal. Relatório entregue ao Instituto Brasileiro de Desenvolvimento florestal. IBDF/DN, Brasília.

Crawshaw P., Quigley H. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. Journal of Zoology 223:357–370.

de la Torre J.A., González-Maya J.F., Zarza H., Ceballos G., Medellín R. 2017a. The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar *Panthera onca*. Oryx 52:1–16.

de la Torre J.A., Núñez J.M., Medellín R.A. 2017b. Spatial requirements of jaguars and pumas in Southern Mexico. Mammalian Biology 84:52–60.

de Souza J.C., da Silva R.M., Gonçalves M.P., Jardim R.J., Markwith S.H. 2018. Habitat use, ranching, and human–wildlife conflict within a fragmented landscape in the Pantanal, Brazil. Biological Conservation 217:349–357.

Desbiez A.L.J., Paula R.C. 2012. Species conservation planning: the jaguar National Action Plan for Brazil. Cat News 7:4–7.

Doran-Sheehy D.M., Fernández D., Borries C. 2009. The strategic use of sex in wild female western gorillas. American Journal of Primatology 71:1011–1020.

Ebensperger L.A. 2018. Strategies and counterstrategies to infanticide in mammals. Biological Reviews 73:321–346.

Goodrich J.M., Kerley L.L., Smirnov E.N., Miquelle D.G., McDonald L., Quigley H.B., Hornocker M.G., McDonald T. 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. Journal of Zoology 276:323–329.

Gottelli D., Wang J., Bashir S., Durant S. 2007. Genetic analysis reveals promiscuity among cheetahs. Proceedings of the Royal Society of London, B: Biological Sciences 274:1993–2001.

Greenberg S., Godin T. 2015. A tool supporting the extraction of angling effort data from remote camera images. Fisheries 40:276–287.

Gross M.R. 1996. Tactics: diversity within sexes. Trends in Ecology and Evolution 2:92–98.

Harmsen B.J., Foster R.J., Sanchez E., Gutierrez-González C.E., Silver S.C., Ostro L.E.T., Kelly M.J., Kay E., Quigley H. 2017. Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; implications for camera trap studies of carnivores. PLoS One 12:e0179505.

Harmsen B.J., Foster R.J., Silver S.C., Ostro L.E.T., Doncaster C.P. 2010. The ecology of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize. In: Macdonald D.W., Loveridge A., editors. The Biology and Conservation of Wild Felids. Oxford University Press; p. 403–416.

Harmsen B.J., Foster R.J., Silver S.C., Ostro L.E.T., Doncaster C.P. 2011. Jaguar and puma activity patterns in relation to their main prey. Mammalian Biology 76:320–324.

Hausfater G., Hrdy S.B. 1984. Infanticide: comparative and evolutionary perspectives. 1st ed. Aldine, New York, USA.

Holt W.V., Pickard A.R., Rodger J.C., Wildt D.E. 2003. Reproductive science and integrated conservation. Cambridge University Press.

Hoogesteijn R., Mondolfi E. 1992. El jaguar, tigre Americano. Ediciones Armitano, Caracas, Venezuela.

Hrdy S.B. 1979. Infanticide among animals: a review, classification, and examination of the implications for reproductive strategies of females. Ethology Sociobiology 1:13–40.

Hunter L. 2019. Carnivores of the world. 2nd ed. Princeton University Press.

Jorge-Neto P.N., Pizzutto C.S., de Araújo G.R., de Deco-Souza T., da Silva L.C., Salomão J.A., Jr., Baldassare H. 2018. Copulatory behavior of the Jaguar *Panthera onca* (Mammalia: Carnivora: Felidae). Journal of Threatened Taxa 10:11391–11398.

Kanda C.Z., Oliveira-Santos L.G.R., Morato R.G., de Paula R.C., Rampim L.E., Sartorello L., Haberfeld M., Galetti M., Ribeiro M.C. 2019. Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use. Journal of Zoology 308:66–74.

Kantek D.N.Z., et al. 2021. Jaguars from the Brazilian Pantanal: low genetic structure, male-biased dispersal, and implications for long-term conservation. Biological Conservation 259:109153.

Kelly M.J., Laurenson M.K., FitzGibbon C.D., Collins D.A., Durant S.M., Frame G.W., Bertram B.C., Caro T.M. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. Journal of Zoology 244:473–488.

Kerley L.L., Goodrich J.M., Miquelle D.G., Smirnov E.N., Quigley H.B., Hornocker M.G. 2003. Reproductive parameters of wild female amur tiger. Journal of Mammalogy 84:288–298.

Lane J.E., Boutin S., Gunn M.R., Slate J., Coltman D.W. 2008. Female multiple mating and paternity in free-ranging North American red squirrels. Animal Behaviour 75:1927–1937.

Larivière S., Ferguson S.H. 2003. Evolution of induced ovulation in North American carnivores. Journal of Mammalogy 84:937–947.

Leuchtenberger C., Crawshaw P., Mourão G., Lehn C.R. 2009. Courtship behavior by jaguars in the Pantanal of Mato Grosso do Sul. Natureza & Conservação 7:218–222.

Logan K.A., Sweanor L.L. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, District of Columbia, USA.

Lyke M.M., Dubach J., Briggs M.B. 2013. A molecular analysis of African lion (*Panthera leo*) mating structure and extra-group paternity in Etosha National Park. Molecular Ecology 22:2787–2796.

MapBiomas. 2020. Collection 5.0 of Brazilian land cover and use map series. http://mapbiomas.org/. Accessed 3 January 2021.

May-Junior J.A., Fagundes-Moreira R., de Souza V.B., de Almeida B.A., Haberfeld M.B., Sartorelo L.R., Rampim L.E., Fragoso C.E., Soares J.F. 2021. Dermatobiosis in *Panthera onca*: first description and multinomial logistic regression to estimate and predict parasitism in captured wild animals. Brazilian Journal of Veterinary Parasitology 30:e023820.

McCarthy M.M., Vom Saal F.S. 1986. Inhibition of infanticide after mating by wild male house mice. Physiology and Behavior 36:203–209.

Michalczyk L., Millard A.L., Martin O.Y., Lumley A.J., Emerson B.C., Chapman T., Gage M.J.G. 2011. Inbreeding promotes female promiscuity. Science 333:1739–1742.

Morato R.G., et al. 2018. Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. Ecology 99:1691–1691.

Morato R.G., Verreschi I.T.N., Guimarães M.A.B.V., Cassaro K., Pessuti C., Barnabe R.C. 2004. Seasonal variation in the endocrine-testicular function of captive jaguars (*Panthera onca*). Theriogenology 61:1273–1281.

Onuma S.S.M., Kantek D.L.Z., Crawshaw P.G., Morato R.G., May-Júnior J.A., de Morais Z.M., Ferreira-Neto J.S., de Aguiar D.M. 2015. Detection of *Leptospira* spp. and *Brucella* abortus antibodies in free-living jaguars (*Panthera onca*) in two protected areas of Northern Pantanal, Brazil. Revista do Instituto de Medicina Tropical de São Paulo 57:177–180.

Packer C., Herbst L., Pusey A.E., Bygott J.D., Hanby J.P., Cairns S.J., Borgerhoff-Mulder M. 1988. Reproductive success in lions. In: Clutton-Brock T.H., editor. Reproductive success: studies of individual variations in contrasting breeding systems. University of Chicago Press; p. 363–383.

Packer C., et al. 2009. Sport hunting, predator control and conservation of large carnivores. PLoS One 4:e5941.

Packer C., Pusey A.E. 1983. Male takeovers and female reproductive parameters: a simulation of oestrous synchrony in lions (*Panthera leo*). Animal Behaviour 31:334–340.

Panthera. 2018. Jaguar corridor initiative. https://www.panthera.org/initiative/jaguar-corridor-initiative. Accessed 18 October 2021.

Paviolo A., De Angelo C., Ferraz K.M.P.M.B., Morato R.G., Pardo J.M., Srbek-Araujo A.C., Beisiegel B.d.M., Lima F., Sana D., da Silva M.X., et al. 2016. A biodiversity hotspot losing its top predator: the challenge of jaguar conservation in the Atlantic Forest of South America. Scientific Reports 6:37147.

Pinho G.M., Fonseca R., Farias I.P. 2014. An opportunity for testing multiple paternity in a wild Jaguar (*Panthera onca*). Biota Neotropica 14:6–10.

Pusey A.E., Packer C. 1994. Infanticide in lions: consequences and counterstrategies. In: Parmigiani S., vom Saal F.S., editors. Infanticide and parental care. Harwood Academic Publishers, Chur, Switzerland; p. 277–299.

Quigley H., Foster R., Petracca L., Payan E., Salom R., Harmsen B. 2017. *Panthera onca* (errata version published in 2018). In: IUCN 2017. The IUCN red list of threatened species. Version 2017: e.T15953A123791436. www.iucnredlist.org. Accessed 10 October 2021.

Core T.R. 2019. R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/.

Rabinowitz A. 1986. Jaguar: struggle and triumph in the jungles of Belize. Arbor House, New York, USA.

Rabinowitz A., Zeller K.A. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biological Conservation 143:939–945.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press.

Seymour K.L. 1989. *Panthera onca*. Mammalian Species 340:1–9.

Sikes R.S., and the The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smith J.L.D., Mcdougal C. 1991. The contribution of variance in lifetime reproduction to effective population size in tigers. Conservation Biology 5:484–490.

Soares T.N., Telles M.P.C., Resende L.V., Silveira L., Jácomo A.T.A., Morato R.G., Diniz-Filho J.A.F., Eizirik E., Brondani R.P.V., Brondani C. 2006. Paternity testing and behavioral ecology: a case study of jaguars (*Panthera onca*) in Emas National Park, Central Brazil. Genetics and Molecular Biology 29:735–740.

Soisalo M.K., Cavalcanti S.M.C. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129:487–496.

Sommer V., Srivastava A., Borries C. 1992. Cycles, sexuality, and conception in free-ranging langurs. American Journal of Primatology 28:1–27.

Stanton L.A., Sullivan M.S., Fazio J.M. 2015. A standardized ethogram for the Felidae: a tool for behavioral researchers. Applied Animal Behaviour Science 173:3–16.

Sunquist M., Sunquist F. 2002. Wild cats of the world. University of Chicago Press.

Thielen D., Schuchmann K.L., Ramoni-Perazzi P., Marquez M., Rojas W., Quintero J.I., Marques M.I. 2020. Quo vadis Pantanal? Expected precipitation extremes and drought dynamics from changing sea surface temperature. PLoS One 15:e0227437.

Tomas W.M., de Oliveira Roque F., Morato R., Medici P., Chiaravalloti R., Tortato F., Penha J., Izzo T., Garcia L.C., Lourival R., ET AL. 2019. Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. Tropical Conservation Science 12:1–30.

Tortato F.R., Devlin A.L., Hoogesteijn R., May-Júnior J.A., Frair J.L., Crawshaw-Jr. P.G., Izzo T.J., Quigley H.B. 2016. Infanticide in a jaguar (*Panthera onca*) population—does the provision of livestock carcasses increase the risk? Acta Ethologica 20:69–73.

United Nations Development Programme [UNDP]. 2021. Jaguar 2030: conservation roadmap for the Americas. https://static1.squarespace.com/static/5bf3393f5b409be1f882f5d4/t/613b670b0e19e4276df263a2/1631282961161/The_Jaguar_2030_Roadmap_final%5B1%5D.pdf. Accessed 20 October 2021.

United States Fish and Wildlife Service [USFWS]. 2018. Jaguar recovery plan (*Panthera onca*). US Fish and Wildlife Service, Region 2, Albuquerque, New Mexico, USA.

Wolff J.O., Macdonald D.W. 2004. Promiscuous females protect their offspring. Trends in Ecology and Evolution 19:127–134.

Wolff J.O., Peterson J.A. 1998. An offspring–defense hypothesis for territoriality in female mammals. Ethology, Ecology and Evolution 10:227–239.

Submitted 17 January 2021. Accepted 6 December 2022.

Associate Editor was Michael Cherry.