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COMMUNICATION

COPULATORY BEHAVIOR OF THE JAGUAR *PANTHERA ONCA* (MAMMALIA: CARNIVORA: FELIDAE)

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COMMUNICATION

Copulatory behavior of the Jaguar *Panthera onca* (Mammalia: Carnivora: Felidae)

Pedro Nacib Jorge-Neto [1], Cristiane Schilbach Pizzutto [2], Gediendson Ribeiro de Araujo [3], Thyara de Deco-Souza [4], Leanes Cruz da Silva [5], Jorge Aparecido Salomão Jr. [6] & Hernan Baldassare [7]

[1,2,6] Department of Animal Reproduction, Faculty of Veterinary Medicine and Animal Science, University of São Paulo (USP) / Av. Prof. Dr. Orlando Marques de Paiva, 87 - Cidade Universitária, São Paulo / SP, 05508-270, Brazil
[3,4] Faculty of Veterinary Medicine and Animal Science, Federal University of Mato Grosso do Sul (UFMS) / Rua Senador Filinto Muller, 2443 - Vila Ipiranga Campo Grande / MS, 79070-900, Brazil
[5] Federal University of Viçosa (UFV) / Avenida Peter Henry Rolfs, s/n - Campus Universitário, Viçosa / MG, 36570-900, Brazil
[7] Department of Animal Science, Faculty of Agricultural and Environmental Sciences, McGill University, 21111 Lakeshore Rd., Ste. Anne de Bellevue, Quebec H9X 3V9, Canada
[1] pepovet@usp.br, [2] cspizzutto@yahoo.com.br (corresponding author), [3] gediendson@gmail.com, [4] thyara.araujo@ufms.br, [5] leanes.c.s@gmail.com, [6] jorgesalomaojr@usp.br, [7] hernanbalda@gmail.com

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Abstract: The relevance of the Jaguar in Brazilian fauna is incompatible with the lack of literature regarding its reproductive behavior, showing that research in this area should be intensified. The knowledge of its basic reproductive behavior is extremely important for understanding the fertility factors of the species and the role it plays in its ecosystem. In this study, we analyzed 210 sequences of sexual behaviors of Jaguars *Panthera onca* starting from proceptivity of the female and ending with copulation; this sequence is called the copulatory behavior. Behavioral sequences were filmed, and the observed behaviors were analyzed and recorded including occurrence frequency. Different behaviors were observed in association with two types of copulation, it was understood that copulation occurs with and without penile penetration. The information found in the present study is valuable for the reproductive management of Jaguars.

Keywords: Copulation, receptiveness, reproduction, sexual behavior.

Abstract / Resumo: Toda a relevância que onça pintada tem para a fauna brasileira é incompatível com a ausência de literatura sobre seu comportamento reprodutivo, mostrando que precisamos cada vez mais intensificar as pesquisas nesta esfera. O conhecimento dos comportamentos reprodutivos básicos é extremamente importante para o entendimento da fecundidade de uma espécie e todo o papel que ela representa dentro do seu ecossistema. Neste trabalho analisamos 210 sequências de comportamentos sócio-sexuais de onça pintada (*Panthera onca*) a partir da proceptividade da fêmea até a finalização da cópula; a esta sequência chamados de comportamento copulatório. As sequências comportamentais foram registradas por filmagens e os comportamentos observados foram registrados por frequência de ocorrência. Diferentes comportamentos foram observados em associação com dois tipos de cópulas, o que nos permitiu concluir que a cópula ocorre com e sem penetração peniana. As informações encontradas serão de grande valia para o manejo reprodutivo da onça pintada.

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INTRODUCTION

The Jaguar *Panthera onca* is one of the most important top predators among Brazilian fauna. This animal's population is decreasing each year due to anthropogenic action, such as fragmentation of its habitat, farming, hunting and slaughter (Cullen et al. 2016; Olsoy et al. 2016; Espinosa et al. 2018). Today, this species is considered as Near Threatened by the IUCN Red List (Quigley et al. 2017) and many research projects involving environmental education, conservation and reproduction with the species have been developed in Brazil, such as NEX No Extinction (Corumbá de Goiás - GO), Projeto Onças do Rio Negro (Aquidauana - MS), Projeto Onçafari (Miranda - MS), Pantera Brasil (Poconé - MT) and Projeto Amigo da Onça (Parque Nacional Boqueirão da Onça - BA), in the attempt to minimize population decrease and negative consequences to Brazilian biodiversity (Tortato et al. 2017; Araujo et al. 2018; Diniz et al. 2018).

Basic information regarding the reproductive behavior of Jaguars is scarce, although this issue is of extreme importance for the development of assisted reproduction and conservation actions. According to Holt et al. (2003) and Owen et al. (2010), reproductive behaviors and subjacent mechanisms associated with reproductive success are particularly important, because fitness is fundamentally a fertility function. For these authors, the study of reproduction is, therefore, crucial for the conservation of species, populations and, indirectly, for the vitality of the entire ecosystem.

Ovulation in this species is usually induced through coitus (Wildt et al. 1979), however, recent studies involving captive females (Gonzalez et al. 2017) reported luteal activity in non-pregnant females that were allocated in individual enclosures, suggesting that spontaneous ovulation occurs occasionally. Interestingly, through hormonal analysis of fecal steroids, Barnes et al. (2016) reported spontaneous ovulations in females housed with males and non-occurrence of spontaneous ovulation in females maintained without the presence of males, demonstrating that the Jaguar is a polyestrous species with induced ovulation.

Stehlik (1971) reported copulatory behavior of the Jaguar at Ostrava Zoo that was briefly described later in 1976 by Lanier and Dewsbury. These authors studied and technically described the copulatory behavior of four *Panthera* species (*P. pardus*, *P. uncia*, *P. tigris* and *P. onca*), concluding that behavioral patterns were qualitatively similar among them, with little variation; however, no study with greater description of such behavior was conducted for the Jaguar.

Limited information regarding copulatory behavior of Jaguars may be justified due to their solitary habits, where interaction with partners is done only during reproductive periods, which makes behavioral studies very difficult with wild animals. On the other hand, the majority of Jaguars kept in zoos and Brazilian rescue centers, present particularities that prevent proper studies with this species, such as animals being too old, castrated, treated with contraceptives or without a reproductive history. One observation of opportunistic courtship behavior, in Pantanal, showed the female's receptiveness and how the male marks the territory before copulatory behavior (Leuchtenberger et al. 2009).

In light of this lack of information concerning the copulatory behavior of Jaguars and its crucial importance for the development of reproductive strategies and assisted reproduction projects, the objective of this study was to analyze a substantial number of sexual interactions of one adult jaguar couple and thereby describe and characterize the reproductive behavior of the captive jaguar.

MATERIAL AND METHODS

We monitored a couple of captive adult Jaguars in the Peter Crawshaw Rescue Center, in southern Pantanal of Brazil. The male Jaguar was four years old and vasectomized; the female was eight years old at the time of the study. The animals' enclosure measured 39m in width and 49m in length. Animals were paired during the entire year and were monitored through cameras Intelbras VDH 5040 VF G2, 24 hours.

A total of 210 films recorded four consecutive natural estrus. Sexual behaviors were registered using the continuous focal method (Martin & Bateson 2007). Moreover, for this study, the proceptivity of the female until the effectiveness of copulation was considered. This sequence of behavioral events was entitled copulatory behavior. A large portion of the methodology for behavioral evaluation was adapted from the classification described by Lanier & Dewsbury (1976), and can be found in Table 1.

Statistical Analyses

Each copulatory behavior sequence, which encompassed the period between female proceptivity and the end of copulation, was considered as one film event. In each film, each behavior (as specified in Table 1) was considered as one registered occurrence.

Table 1. Behavioral catalog used for the description of the copulatory behavior of the couple of Jaguars *Panthera onca* at the Peter Crawshaw Rescue Center, in southern Pantanal

Sexual behavior	Definition
Pre-copulatory vocalization of the female	When the female vocalizes during proceptiveness
Copulatory vocalization of the female	When the female vocalizes during the copula
Vocalization of the male	When the male vocalizes during the copula
Attractiveness of the male	When the male approaches the female and initiates the interaction that may lead to the copula
Proceptiveness of the female	When the female requests the male, approaching and turning to him, with presentation of the anal-genital region;
Receptiveness of the female	When the female accepts mount from the male
Squatting of the female	When the female squats in ventral decubitus, in sexual receptiveness posture
Biting or licking of the male on the females nape	When the male licks or bites the females nape during the copula
Rocking of the female	When the female, after the copula, turns around and hits the male with one paw
Rolling of the female	When the female rolls into lateral dorsal decubitus after the copula
Copula without penial introduction	When the pelvic movement of the male occurs during the mount on the female, however, without introduction of the penis
Copula with penial introduction	When the pelvic movement of the male occurs during the mount on the female, followed by the introduction of the penis.

At the end of each film, a quantitative analysis of occurrence frequency (%) was performed for each behavior presented in relation to the total occurrences in all filmed sequences. Further analysis of copulatory behaviors between event ending with vs. without penile penetration was conducted by contingency analysis and Fisher's exact test. Differences were considered to be statistically significant at the 95% confidence level ($P<0.05$).

RESULTS

The duration of each estrus period based on female receptivity were nine, eight, eight and 10 days for the four estrus cycles evaluated and the estrus-to-estrus interval was 34, 39 and 30 days. The visualization and consequent confirmation of penile introduction during copulation occurred in 10 episodes. All behavior sequences observed during female receptivity (210 events) until the end of the male´s pelvic movement behavior were similar. The analysis of the male's pelvic movement behavior showed two different behavioral sequences, characterized as copulatory behavior with penile penetration (122 events) and copulatory behavior without penile penetration (88 events).

In the sequence of copulatory behavior without penile penetration, the male left the female after finishing his pelvic movements in 42% of the sequences observed. In turn, in the sequence with penile penetration, additional copulatory behaviors were observed from this moment on, such as the male biting or licking the female's nape, and female rocking and rolling in lateral-dorsal decubitus in 58% of observations. The frequencies of sexual behavior occurrences that involved both Jaguars' copulatory behavior sequences can be observed in Figure 1:

- The positioning of the female (squatting) was verified in 100% of our observations;
- Male vocalization was observed in only 1/88 copulatory events without penetration ($P<0.001$);
- High copulation frequency could be partly explained by the fact that penile penetration occurred only in 42% of the mounts;
- Female vocalization during proceptivity occurred at practically the same frequency preceding copulations with and without penile penetration (55% and 45%, respectively; $P>0.05$);
- During copulation, female vocalization was more frequent when there was penetration (95.1% vs. 79.6%, $P<0.01$);

When penile penetration could be confirmed, the copulatory behavior presented the following sequence of events:

- Proceptivity of the female with tail movement and presentation to the male (Figure 2.1)
- The female lies in ventral decubitus, deviating the tail to the side and exposing the anal-genital region to the male; the thoracic limbs of the female are, in general, elongated and the pelvic limbs are flexed next to the body (Figure 2.2)
- The male mounts from the back and on top

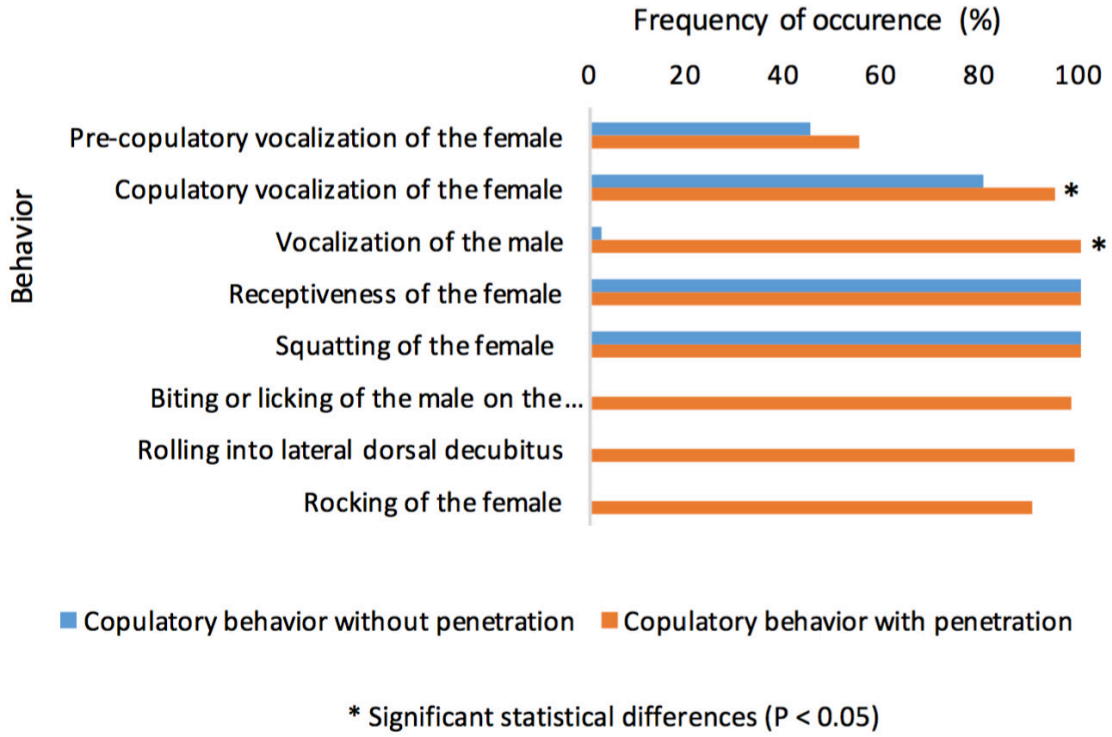

Figure 1. Frequencies of occurrences of the behavioral events found in the copulatory behavior of the Jaguar *Panthera onca*.

of the female, keeping her between his front paws. He then approximates his genital region to the female's, squatting with the pelvic limbs

- The female deviates the tail and the male initiates pelvic impulse – the penis is introduced – the male bites/licks the female's nape three or four times (Figure 2.3) – the female may or may not emit a low growling – the male roars, presumptively indicating ejaculation
- Female rocking – rolling into lateral dorsal decubitus (Figure 2.4).

DISCUSSION

The results found in this study represent the first complete descriptions of the copulatory behavior specific to the Jaguar *Panthera onca* since the 1970s, which is information of great relevance for studies involving biology and even reproductive biotechnologies. In this context, the understanding of reproductive behaviors and aptitude of any species is critical for the understanding fertility (Owen et al. 2010).

One opportunist observation (Leuchtenberger et al. 2009) and previous studies from Lanier & Dewsbury (1976) and Stehlik (1971) reported rudimentary information regarding the reproductive behavior of the genus *Panthera*, but only part of these reports involving copulation in the genus *Panthera* can be considered specifically for the Jaguar.

By initiating observations from the moment the female shows herself as proceptive to the male, it was clear that the percentage of approach from the male to the female corresponded exactly to the percentage of female proceptivity, thereby indicating that female signalization for possible receptiveness is highly effective in triggering male attractiveness and initiation of courting.

From the moment when the female was receptive to the male and male pelvic movements began, in 42% of the sequences observed, the male finished the copulatory behavior and left the female. This supported the conclusion that this would be a copulatory behavior without penile penetration. In 58% of observations, the male remained in the act of copulation and started biting or licking the female's nape. In turn, the female started rocking and rolling in lateral-dorsal decubitus. In this situation, we concluded that penile penetration occurred. When penile penetration occurred, the male vocalized in 100% of the events before lightly biting or licking the female's nape, as described by Hancock (2000) for leopards and by Lanier & Dewsbury (1976)

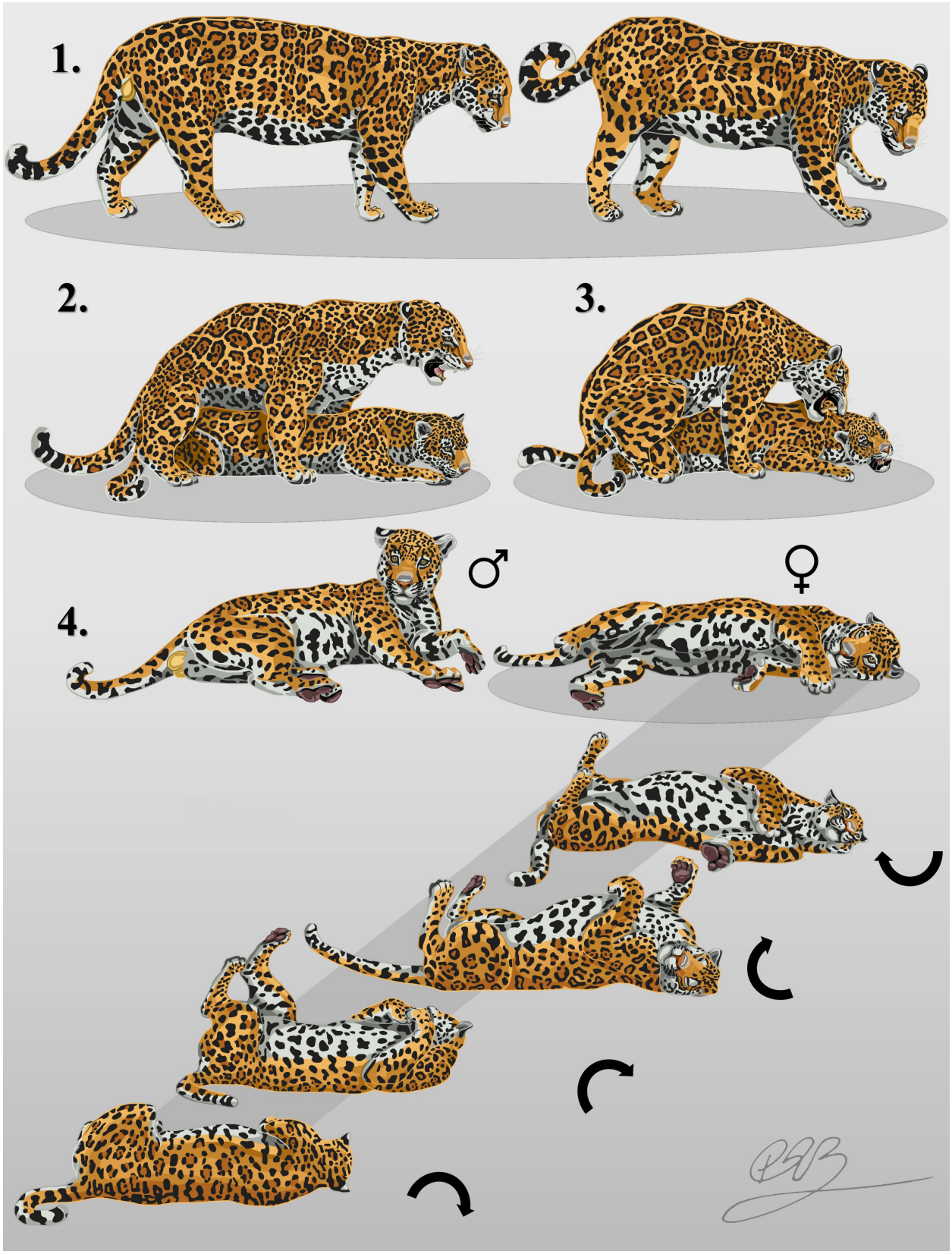

Figure 2. Schematic diagram of copulatory behavior of the Jaguar *Panthera onca*: 2.1 (Proceptivity of the female with tail movement and presentation to the male), 2.2 (Proceptivity of the female with tail movement and presentation to the male), 2.3 (The female deviates the tail and the male initiates pelvic impulse – the penis is introduced – the male bites/licks the female's nape), 2.4 (Female rocking – rolling into lateral dorsal decubitus) – Illustrator: Pedro Busana

for Jaguars. In contrast, male vocalization was observed in only 1/88 copulatory events without penetration (P<0.001). These findings are consistent with the study by Lanier & Dewsbury (1976), who described that the males' roar during copulation was verified in every observation of copulation with penile penetration, signalizing success in ejaculation.

It is interesting to point out that the elevated number of copulations in felid species, according to Wildt et al. (2010), has been proposed as a method to induce multiple ovulations among females, and also, in species with high incidence of teratospermia, to ensure deposition of an adequate amount of normal sperm in the vagina, thereby increasing the chance of pregnancy.

According to other comparative in situ and ex situ studies, when compared with others wild felid species such as Cheetahs (Crosier et al. 2009), Clouded Leopards (Wildt et al. 1986), and Oncillas (Swanson & Brown 2004) teratospermia (>60% of defective spermatozoids) is not common in the Jaguar (Morato et al. 2001; Araujo et al. 2018; Gonzales et al. 2017) . Nevertheless, multiple copulations were observed in the present study. High copulation frequency could be partly explained by the fact that penile penetration occurred only in 42% of the mounts, so the male continued attempting to mount until completing ejaculation. Nevertheless, we believe that future studies must be conducted in a format allowing the confirmation of semen deposition in the vagina.

Every positioning of the female, described by Lanier & Dewsbury (1976), such as squatting (elongated anterior limbs and flexed posterior limbs next to the body) was verified in 100% of our observations, both for copulations considered as "with" and "without" penetration. This suggests that the success of penile penetration is not related to female posture, because the female was found in the same position in both situations.

Female vocalization during proceptivity did not influence the result of copulation since it occurred at practically the same frequency preceding copulations with and without penile penetration. During copulation, however, female vocalization was more frequent when there was penetration. Only when copulation involved penile penetration was the female rocking followed by rolling into lateral dorsal decubitus. These findings are consistent with observations by Stehlik (1971) but in disagreement with report by Lanier & Dewsbury (1976), who did not describe female rolling into lateral dorsal decubitus as characteristic behavior after copulation.

CONCLUSIONS

- Basic information regarding the reproductive behavior of Jaguars is of extreme importance for the management, development of assisted reproduction and conservation projects.

- Copulatory behavior of the Jaguar was described in a qualitative manner starting from first signs of female proceptivity and until the finalization of copulation.

- We found that close to half of the copulation events of *Panthera onca* might occur without penile penetration and, in these cases, ejaculation is believed not to occur.

- Numerous copulations occured during female estrous. Consistent with thoughts reported by others, we believe this behavior may be necessary to promote multiple ovulations and to ensure sufficient number of successful penile penetrations with ejaculation, thereby ensuring proper numbers of normal fertilizing sperm are deposited in the vagina.

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Author Details: Pedro Nacib Jorge Neto, DVM, MBA. Actually master's degree student (PPGRA-FMVZ / USP) and Technical-Commercial Director of IMV Technologies Brazil. Member of REPROCON research group. Cristiane Schilbach Pizzutto, DVM, MSc, PhD, Postdoc. Professor at FMVZ/USP. Chairman of the Animal Welfare Committee of CRMV - SP. Member of the International Environmental Enrichment Conference Committee and of REPROCON research group. Gediendson Ribeiro de Araujo, DVM, MSc, PhD, Postdoc. Veterinarian at UFMS. Expert in scientific capture of free-living felids. Member of REPROCON research group. Thyara de Deco-Souza, DVM, MSc, PhD. Professor at FAMEZ/UFMS. Expert in morphophysiology of reproduction of wild and domestic animals. Member of REPROCON research group. Leanes Cruz da Silva, DVM, MSc, PhD. Expert in carnivore conservation. Jorge Aparecido Salomão Jr., DVM. Actually master's degree student (PPGRA-FMVZ / USP). Works with clinic and surgery of wild and exotic animals in private clinics. Member of REPROCON research group. Hernan Baldassarre, DVM, PhD. Professor at McGill University (Canada). Expert in small ruminants reproduction. Global consultant for animal breeding companies. Member of REPROCON research group.

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