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A systematic review of reproductive physiology of jaguars (*Panthera onca*)

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ABSTRACT

The jaguar (*Panthera onca*), the largest felid in the Americas, has been classified by IUCN as 'near-threatened'. The purpose of this review was to gather the current knowledge on jaguar reproduction. Information from over forty-five sources has been selected. Jaguars have been classified as polyestrous with generally an induced ovulation, with a moderate incidence of spontaneity. Estrus, estrous cycle and pseudopregnancy lengths varied from 4 to 17, and 22–63, and 14–67 days, respectively. Ejaculate volume is around 3.9 ml and the spermatogenic cycle takes 57.7 ± 0.07 days. In spite of its low gonadosomatic index, the whole spermatogenic process in jaguars is more efficient than that of the domestic cat. Although minor seasonal variation in most reproductive traits has been found at the studied latitudes, local rains seemed to have an effect. Gestation takes from 91 to 111 days. Females queen one to four immature cubs. As evidenced by the wide range reported for most reproductive parameters further work is still necessary to achieve fundamental knowledge that could facilitate breeding, management and conservation activities.

Introduction

The jaguar (*Panthera onca*) is the largest felid in the Americas, being the only one of the five members of genus Panthera in the continent. Jaguars, which are native to the Americas, are key components of ecosystems as they help to maintain biodiversity and ecological processes via multiple food web pathways [1]. Jaguars are strong felids adapted to their diet [2,3]. As obligate carnivores their feeding behavior varies according to prey density and ease of prey capture [2].

According to Jedrzejewski et al. (2018; [4]), currently the world's jaguar population is estimated at 173,000 individuals, with Brazil being the most important country for this felid, as the holder of half of the world's population with approximately 86,800 animals, followed by Peru with as many as 22,200 [4,5]. Despite the fact that jaguars have been eliminated from many parts in the world during the last fifty years and their habitats have been markedly reduced, this felid still ranges from Central America to eastern Colombia, Venezuela, Suriname, the Guaianas, Brazil, and further south into Peru, Bolivia, the Paraguayan Chaco and northern Argentina [3]. The jaguar is mainly a solitary, opportunistic, apex predator that is not preyed upon. They live in delimited territories from 10 to 40 km^2, with the range being dependent on the availability of food and water [6].

Similar to most wild felids, the jaguar is classified as 'near-threatened' under the International Union for Conservation of Nature (IUCN; [7]), declared as an 'endangered' species under the US Endangered Species Act (ESA) and the Red Book of threatened mammals of Argentina [8], and listed under Appendix I by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) [9].

Although, most felid species reproduce poorly in captivity, captive breeding can provide a safeguard against extinction. Even though, the reproductive potential of *ex situ* individuals can be maximized through natural breeding and implementation of assisted reproductive techniques [10], data on the reproductive biology of jaguar remain scarce when compared to the knowledge obtained in other large felids. Information of reproductive parameters in free-living populations is even more scarce. Understanding the reproductive patterns of jaguars is a critical factor for predicting both the sustainability of wild populations and the viability of reproductive programs in captivity [11].

The aim of this article was to review the main reproductive physiological aspects of jaguars that will be useful for designing future reproductive studies in this species. Whenever possible, comparisons with the traditional feline model, the domestic cat (*Felis catus*) was also performed.

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Methods

International peer reviewed publications were downloaded for the period from 1950 to 2022. Searches were conducted in Pub Med, Scholar Google, Google, Science Direct, ProQuest and Scielo using the following search terms: common name “jaguar’ OR ‘Panthera onca” OR ‘felid” AND “reproduc* ” OR “female” OR “male” OR “estrous cycle” OR “estrus” OR “pregnan* ” OR “gestat* ” OR “semen” OR “spermato* ” OR “copulat* ” OR “reproduc* behav* ”.

Findings

A total of 191 publications were retrieved from Pub Med. Forty-seven bibliographical sources were considered relevant to the topic and, therefore, selected. From these forty-seven sources, six were general feline reviews, one was a review on other species and two were meta-analysis articles, while thirty were original research articles. These studies were longitudinal, retrospective (one) and prospective (twenty-nine) descriptive studies. Finally, one case report, two master thesis, four book chapters and one international association web sites were found eligible for this review.

Sixteen of the original research articles were about jaguar reproduction. Three articles corresponded to female jaguar reproduction, seven to male and six to a combination of both genders. Fourteen publications were carried out in captive felids, and two in both captive and free-living animals. The number of studied jaguars in each article ranged from 1 to 15, with a mean ± SD of 5.81 ± 4.15 and their age varied from two to twenty years, with only four prepubertal animals being followed up. All studies were performed between 37°19′32.27″ N and 30°01′58″ S latitude except two reports. The two reports out of this latitude range were at 51°32′08″ N and 49° 50′ 44″ N. One, twelve and three publications were placed in the Equatorial, Tropical and Temperate zones, respectively.

General biometric data and longevity

Jaguars are deep-chested, with large head, powerful bite and sturdy limbs [3]. Their coat is pale yellow to tan or reddish-yellow with whitish ventral areas and darker spots - rosettes - on the sides, which serve as camouflage in vegetation [3]. Jaguars can grow up to 182 cm long, without the tail, which can be up to 75 cm long [2]. Males can weigh 120 kg and females 72 kg, but their body weight can vary among regions. In general terms, females are 10–20% smaller than males, which is the major sexual dimorphic feature [3]. In the wild, jaguars live about 10–12 years, but there are some cases that lived up to 15–16 years. In captivity, however, they can exceed 20 years of age [2].

Female reproduction

Anatomy of the female genital tract

Although larger, the jaguar resembled the domestic cat with respect to reproductive tract anatomy [12,13]. Ovarian follicle and corpora lutea morphology are also similar in appearance to those of the domestic queen [12,14]. At estrus, ovoid ovaries of about 3.5 cm in diameter containing about 3–4 non-protruding spherical 3–6 mm follicles. At the luteal phase dark orange to pale yellow corpora lutea (8–10 mm) were progressing to corpus albicans of less than 1 mm diameter [12].

Estrus cycle and hormone analysis

Felids have been traditionally categorized as polyestrous and induced ovulators -requiring mating to stimulate ovulation. Also, jaguars have been classified as polyestrous and generally induced ovulators, albeit with a moderate incidence of spontaneous ovulation (see below; [10,11,14]).

As serial blood sampling is impractical in stress-susceptible wild felids, hormonal characterization of the reproductive cycles has been conducted using noninvasive longitudinal monitoring of steroids in feces. Importantly, in felids, a large percentage of steroid hormone metabolites are excreted through feces [15]. Increases of fecal estrogens to four times basal concentrations can be used, retrospectively, to distinguish estrus from interestrous periods. Progestin rise is proof of ovulation and indicative of the consequent pregnant or non-pregnant luteal phase [16]. The secretion of progestins is necessary for maintaining the pregnancy, and are firstly produced by the corpora lutea and later by the placenta [17]. As both basal and peak hormone concentrations differed among publications due to the different analytical methods or antibodies used, hormonal values were mostly avoided in this review.

Puberty and estrus behavior

Estrus can also be detected by observing overt behavioral changes, but this requires a solid knowledge of the behavior of a particular species. It is also time consuming to observe the animals or their films.

In a longitudinal fecal analysis of sexual steroid hormones in three, 10–15 year female jaguars which were confined individually in the Colombian zoological park of Santacruz (Cundinamarca, Colombia; latitude 4°35'0.65"N) a significant negative effect of local rains was found on reproductive seasonality [11]. Thus, the lowest fecal concentrations of estradiol and progestins were found during the last three rainy months of the year. During this wet period, anestrus lasted between 31 and 83 days [11].

According to the Guidelines of the Jaguar SSP Management Group [18], females reach sexual maturity at about 24 months of age [18]. In a study conducted during 18 months in the Parque Zoológico Municipal Quinzinho de Barros (Sorocaba, Brazil, 23°30′21″S) and the Centro de Conservaç ão da Fauna Silvestre Ilha Solteira (São Paulo, Brazil, 20°24'56.11"S) in three captive females, exposed to natural climatic conditions, sexual maturity was attained within 18 and 20 months of age [19]. In this study, significant differences between pre-pubertal and adult fecal estrogen and progestin concentrations confirmed pubertal achievement. Importantly, in that study, there was an absence of behavioral estrus at the peripubertal period [19]. Wildt et al. (1979; [12]) described puberty by behavioral assessment in one female housed isolated in an outdoor, covered cage enclosure in the Gladys Porter Zoo (Brownsville, Texas, USA; latitude: 25°54'47.98"N) to be 29.5 months [12].

Wildt et al. (1979; [12]) reported, in the female mentioned above, the mean duration of estrous cycle as 47.2 ± 5.4 days when behaviorally observed during 7 cycles (Table 1; [12]). This wide range suggests that some cycles could have been missed. More recently, in two captive adult females of the Fundaç ão Parque Zoológico de São Paulo (São Paulo, Brazil; latitude: 23°39′03″S) and the Fundaç ão RioZoo (Rio de Janeiro, Brazil; latitude: 22°54′16″S) that were followed up by fecal analysis for seven estrous cycles during 18 months, the whole cycle length was 38.28 ± 2.52 days (Table 1; [19]). Stehlik (1971; [20]) described three females housed with a male at the Zoologická zahrada a botanický park (Ostrava, Czech Republic, latitude: 49°50′44″N) in which behavioral estrus recurred every month (Table 1; [20]).

The estrous behavior of jaguars takes the same course as that of other big cats i.e. the females growl, rub against objects and roll on the ground, to increase restlessness and pacing and vocalization [12,20].

Sadleir et al. (1966; [21]) reported the length of behavioral estrus in a female housed continually with a male in the London Zoological Gardens, Regent’s Park (UK; latitude: 51°32′08″N) as 12.9 days (Table 1; [21]). Wildt et al. (1979; [12]), in the previously mentioned study, described estrous behavior lasting 12 ± 1 days (Table 1; [12]). Barnes et al. (2016; [10]) carried out a study in which seven 6–18 year old jaguars housed at five different institutions: Jacksonville Zoo and

Table 1
Estrus cycle length and estrus length.

Location	Animals (n)	Duration of estrus cycle (days)		Duration of estrus (days)		Authors
		Hormonal[a]	Behavioral[b]	Hormonal[a]	Behavioral[b]	
London Zoological Gardens, United Kingdom (latitude: 51°32′08″N)	1	–	42.6 (range 26–60)	–	12.9 (range 6–17)	Sadleir (1966;[21])
Zoologická zahrada a botanický park Ostrava, Chez Republic (latitude: 49°50′44″N).	2	–	33.2 (range 22–58)	–	7.8 (range 5–11)	Stehlik (1971;[20])
Gladys Porter Zoo, USA (latitude: 25°54′47.98″N)	1	–	47.2 ± 5.4 (range 31–63)	–	12.0 ± 1.0	Wildt et al. (1979; [12])
Jacksonville Zoo and Gardens, USA (latitude: 30°24′14.67″N) Zoo Miami, USA (latitude: 25°36′42.36″N) Memphis Zoo, USA (latitude: 35° 8′59.71″N) Oklahoma City Zoological Park, USA (latitude: 35°31′25.67″N) Happy Hollow Park and Zoo, USA (latitude: 37°19′32.27″N)	7	–	–	6.5 ± 0.3	7.8 ± 0.7 (range 4–11)	Barnes et al. (2016; [10])
Peter Crawshaw Rescue Center in southern Pantanal of Brazil (16° to 20° S).	1	–	34.3 ± 4.5 (range 30–39)	–	8.75 ± 0.95 (range 8–10)	Jorge Neto et al. (2018;[22])
Fundação Parque Zoológico de São Paulo, Brazil (latitude: 23°39′03″S) Fundação RioZoo, Brazil (latitude: 22°54′16″S)	2	38.28 ± 2.52 (range 25–44)	–	10.42 ± 1.15 (range 7–15)	–	Viau et al. (2020; [19])

[a] Determination by fecal samples
[b] Determination by behavioral observations

Gardens (Jacksonville, Florida, USA, 30°24′19″N) ($n = 3$; ages 6–18 years, housed with physical or visual access to females and males), Zoo Miami (Miami, Florida, USA, 25°36′42.36″N) ($n = 1$; age 6 years, housed with visual access to another female and a male), Memphis Zoo (Memphis, Tennessee, USA, 35° 8′59.71″N) ($n = 1$; age 7 years; housed with another female), Oklahoma City Zoological Park (Oklahoma City, Oklahoma, USA, 35°31′25.67″N) ($n = 1$; 8 years of age; housed with physical access to a male only during estrus), and Happy Hollow Park and Zoo (San José, California, USA, 37°19′32.27″N) ($n = 1$; 6 years old; housed alone). All females had exposure to natural day length and temperatures. In each case, both fecal estrogen metabolite analyses and behavioral assessments were used. Thus, estrus length, according to 194 hormonal determinations, was 6.5 ± 0.3 days and on behavioral observations was 7.8 ± 0.7 days (Table 1; [10]). Hormonal characterization of estrus was also carried out by Viau et al. (2020; [19]) in the previously described female jaguars. These authors established estrus length as 10.42 ± 1.15 days (Table 1; [19]). Jorge Neto et al. (2018 [22]) used cameras to monitor a couple of captive adult jaguars in the Peter Crawshaw Rescue Center in southern Pantanal of Brazil (latitude: from 16–20°S). The male jaguar was vasectomized and the female was 8 years old. Four consecutive natural estruses were followed. The mean duration of each estrus period was 8.75 ± 0.95 and the estrus-to-estrus interval were 34, 39 and 30 days (Table 1; [22]).

Ovulation, luteal phase and pseudopregnancy

Previous observations suggested the jaguar is primarily an induced ovulator [12]. Barnes et al. (2016; [10]) describes the occurrence of elevated fecal progestins on five occasions in females without exogenous stimulation [10]. More recently, Jimenez Gonzalez et al., (2017 [11]) reported luteal activity in non-pregnant female jaguars that were allocated in individual enclosures, suggesting that spontaneous ovulation occurs occasionally [14]. Jorge-Neto et al. (2020 [14]) reported that the nearby presence of males can also induce ovulation through the visual, olfactory and/or auditory senses in the seven captive females they studied [14].

During the luteal phase, one or more corpora lutea produce progesterone that remains elevated for varying lengths of time depending on whether conception occurs or not. Progestin concentrations during pregnant and nonpregnant luteal phases are quantitatively similar in nondomestic felids as in the domestic cat [13,23].

In jaguars, pseudopregnancy (defined as long luteal phases after ovulation) may occur after an infertile mating, early pregnancy termination [23] or spontaneously. Barnes et al. (2016; [10]) analyzed fecal progestin concentrations to characterize the average length of pseudopregnancy. These authors described three episodes of pseudopregnancy in two females which had previously experienced vaginal stimulation and five episodes of spontaneous pseudopregnancies in females that were housed in the presence of males. Mean length of physically induced and spontaneous pseudopregnancies were 24.7 ± 4.2 days and 29.6 ± 2.6 days, respectively [10]. Jimenez Gonzalez (2017; [11]) reported non-pregnant luteal phases ranging between 14 and 67 days also based on increased fecal progestine [11].

Pregnancy and cubs

Cats have an endotheliochorial type, zonary placenta and do not produce chorionic gonadotropin [13]. In captivity, births of jaguar cubs have been reported throughout the year; this may also hold true for wild animals living in Tropical and Temperate zones. However, in more northerly and southerly areas the seasonal effect is more evident. Thus, births are more common in Paraguay from November to December, in Brazil from December to May, in Argentina from March to July, in Mexico from July to September, and in Belize from June to August [2].

Jaguar gestation period is generally 91–111 days and litter size is usually 1–4 cubs [18]. The mean age of the female jaguar at the last

gestation is about 8 years [2]. Studies in captivity reported females giving birth to singleton cubs [10,21] after 93–105 days [10,24] and 108–111 days [21] of gestation. Barnes et al. (2016; [10]) reported that estrus resumption occurred approximately 15 days post-partum [10]. Conversely, Stehlik (1971; [20]) described the first estrus one month after weaning i.e., 6 months after parturition [20].

The females give birth in secluded sites [2]. As females separate from males immediately after mating, they have to provide all parenting to the newborns [18]. The altricial cubs weight about 600–900 g at birth; cubs open their eyes after one week and are weaned at the age of three months. They remain with their mother for a period of approximately two years [18].

It is possible to diagnose pregnancy based on fecal progestin concentrations that remain elevated past the normal length of a non-pregnant luteal phase [13]. Progesterone concentrations are similar during both non- pregnant and pregnant luteal phases. As non -pregnant luteal phase is approximately half to two thirds the duration of the pregnant luteal phase in most felids, gestation can be confirmed by detecting elevated progesterone concentrations rather late in gestation, thus its practical application is limited [13,25].

Male reproduction

Anatomy and puberty

Male jaguar is generally sexually mature at the age of 2–3 years [18]. The mean testis weight for the adult jaguar was reported to be 17.7 ± 2.2 g [26]. Gonadosomatic index ranged from 0.05 ± 0.01% [26] to 0.034% [6,27].

Hormone analysis and seasonality

Morato et al. (2001; [28]), compared serum testosterone from six free-living and eight captive male jaguars. Blood collection was attempted on seven occasions from six free-living jaguars captured at Porto Primavera area (São Paulo, Brazil, 22° 014′S, $n = 4$), Emas National Park (Goiás, Brazil, 18° 19′S, $n = 1$) and Iguaçu National Park (Misiones, Argentina, 25°05′S, $n = 1$). The mean estimated age of these jaguars was 5 ± 1 years [28]. The captive-born male jaguars were maintained in individual cages at São Paulo Zoo (São Paulo, Brazil, 23°39′03″S, $n = 5$) or paired with a male or female at the Parque Zoológico Municipal Quinzinho de Barros (Sorocaba, Brazil, 23°30′21″S, $n = 3$). Mean age of these animals was 7 ± 1.5 years. The felids were restrained at 2-month intervals to obtain blood samples [28]. Samples were analyzed by a single radioimmunoassay and serum testosterone concentrations for captive jaguars and for free-living jaguars, did not differ [28].

Longitudinal profiles of fecal androgen metabolites, which were collected one to three times per week during 7–14 months, were described in six captive male jaguars by the same authors [29]. Their ages ranged from 3 to 10 years. The males were maintained in individual outdoor cages with indirect olfactory or visual contact at Sao Paulo Zoo (Brazil, 23°39′3.2″ S) ($n = 3$) or paired with a male ($n = 2$) or female ($n = 1$) at the Sorocaba Zoo (Brazil, 23°30′21″S). There was considerable variation among individual fecal androgen concentrations [29]. In the same study, to assess seasonality, data were grouped according to standard seasons and also to local rains as dry season and wet season. There were no differences among the standard seasons of the year in fecal androgen concentrations. However, fecal androgen concentrations appeared higher in the wet season [29].

Reproductive analysis of two adult captive jaguars aged 10–20 years at the Santacruz Zoological Foundation (Cundinamarca, Colombia, 4°35′0.65″ N) was conducted by performing a longitudinal, non-invasive, fecal hormonal analysis over the course of a year. When these concentrations were compared among the four local Equatorial seasons i.e. rainy 1, dry 2, rainy 2 and dry 1 no significant differences were found among them [11].

Spermatogenesis and morphometric values

Costa et al. (2008; [26]) analyzed four adult animals weighing 77 ± 3 kg from zoos located in the cities of Rio de Janeiro (Brazil, 22°54′30″S) and Porto Alegre (Brazil, 30°01′58″S) without taking season into account. Tissue samples from testicles were routinely processed for histological, morphometric, and autoradiographic evaluation. The duration of the spermatogenic cycle was estimated based on stage frequencies. Based on the tubular morphology system eight stages of the spermatogenic cycle were characterized, the seminiferous epithelium cycle for the two animals investigated was estimated to be 12.8 ± 0.01 days. Thus, the whole spermatogenic process for jaguars would take approximately 57.6 days [26].

When volumetric proportions of the different testicular parenchyma components were described for the jaguar, seminiferous tubules, intertubular tissue and Leydig cells were 77%, 23% and 13%, respectively [27]. Costa et al. (2008; [26]) described similar volumes for jaguar seminiferous tubules and Leydig cells: 74.7 ± 3.8 and 16.7 ± 1.6%, respectively [26].

In jaguars, the length of seminiferous tubule is 12.2 m per gram of testis, which is within the range (10–15 m/g) described in most domestic animals [27,30]. Jaguar seminiferous tubular diameter is 257 μm [6,27], which is also within the range of mammals (180–350 μm) including the domestic cats [27,31]. Seminiferous epithelium height varies from 81 to 90 μm in the jaguar [27,31].

The efficiency of spermatogenesis is estimated by different indexes among spermatogonia A and the other germinal cells by transverse section of seminiferous tubules [26]. In jaguars, about 9.2 primary preleptotene spermatocytes are produced from each spermatogonium A (mitotic index; [27]). Azevedo (2004; [6]) described a meiotic yield for jaguars of 3.2 ± 0.35 representing a loss of 20% in the expected number of round spermatids [27]. Finally, the intrinsic efficiency of spermatogenesis in this species is about 23.4 round spermatids [6,27].

Sertoli cells play a fundamental role in spermatogenesis [30]. Sertoli cells index (Sertoli cells: round spermatids) varies among species and when the rate is high, sperm production is also high [30]. Sertoli cell efficiency in jaguars, estimated from the total number of germ cells and the number of round spermatids per Sertoli cell, was 18.7 ± 2.6 and 7.9 ± 1.5, respectively [26]. According to Costa et al. (2006; [27]) in jaguars, each Sertoli cell supports approximately 19.2 germ cells and 11.01 round spermatids (Sertoli cell index; [27]). The number of Leydig cells - responsible for androgen production - per gram of testis was 107 ± 12 × 10^6 in male jaguars [26].

Seminal parameters

In the study carried out by Silva et al. (2019; [32]) analyzed spermatozoa of five captive adult male jaguars. The ages of these males varied from 4 to 17 years old and mean body weight was 70.8 ± 5.9 kg. The animals were housed alone ($n = 1$) or with a female ($n = 4$) at five different Brazilian zoos: Ecological Park – Eco-Point (Fortaleza, CE, Brazil 3° 43' S); São Francisco Zoo (Canindé, CE, Brazil, 4° 21' S); Teresina Zoobotanical Park (Teresina, PI, Brazil, 5º 05' S); Arruda Câmara Zoobotanical Park (João Pessoa, PB, Brazil, 7º 06' S) and Dois Irmãos Park (Recife, PE, Brazil, 8º 03' S). In this study, spermatozoa head appeared slightly oval shaped, 3.6 ± 0.03 μm wide and 4.9 ± 0.02 μm long. The length of the intermediate piece was 9.7 0.3 μm, and the length of the tail was 54.5 ± 0.1 μm. The total length of the sperm cell in this species was 59.5 ± 0.1 μm, with high homogeneity within individuals [32].

Jimenez Gonzalez et al. (2017; [11]) conducted a seminal analysis in the three male jaguars of the previously described study. Collection was carried out by means of electro-ejaculation in two males and one through postmortem epididymal flush, with one sample for each animal [11]. Seminal values are shown in Table 2.

Table 2
Seminal analysis.

Location	Animals (n)	Body weight (kg)	Testicular volume (cm^3)	Collection Technique[a]	Semen volume (ml)	Sperm concentration (x 10^6)	Total spermatozoa/ ejaculate (x 10^6)	Sperm motility (%) and rate of progressive status (0–5)		Normal spermatozoa (%)	Authors
Porto Primavera area (22° 014′S, n = 4), Emas National Park (8° 19′S, n = 1) and Iguaçu National Park (25°059′S, n = 1), Brazil	6 (wild)	96.0 ± 7.7	52.4 ± 3.4	EE	4.1 ± 0.7	35.0 ± 21.3	152.0 ± 88.0	73.0 ± 6.1	3.5 ± 0.2	73.5 ± 3.9	Morato et al. (2001;[28])
São Paulo Zoo (23°39′03″S, n = 5) and Sorocaba Zoo (23°30′21″S, n = 3), Brazil	8 (captive)	72.0 ± 11.0	41.6 ± 0.6	EE	8.3 ± 0.7	8.0 ± 1.7	59.3 ± 12.8	64.0 ± 2.4	2.8 ± 0.1	50.0 ± 1.1	
Sao Paulo Zoo, Brazil (23°39′3.2″ S) and Sorocaba Zoo, Brazil (23°30′21″S)	5 (captive)	70.5 ± 4.5	44.4 ± 2.0	EE	6.60 ± 1.9	6.30 ± 2.4	–	57.0 ± 4.5	2.80 ± 0.2	60.8 ± 3.1	Morato et al. (2004;[29])
Santacruz Zoological Foundation, Colombia (4°35'0.65"N)	3 (captive)	53 ± 2.6	–	EE and EF	Range: 1.5–2.5	5.7 ± 1.1	–	80	–	80 ± 2.8	Jimenez Gonzalez et al. (2017; [11])
Taiamã Ecological Station (16°50'34.83"S) Barranco) Alto Farm (19°34'38.58"S), and Pantanal and Serra da Capivara National Park in Caatinga (8°46'3.05"S), Brazil	5 (wild)	95.8 ± 35.4	–	UC after ME	0.43 ± 0.262	3315 ± 114-1.67	1280.75 ± 5-78.53	81 ± 7.4	3.9 ± 0.54	51.0 ± 22.8	Ribeiro de Araujo et al. (2018;[33])
Mata Ciliar Association (23°10'41.30"S), Paulínia Zoo (22°45'58.40"S), and organization NEX (15°51'33.29"S), Brazil	6 (captive)	61.7 ± 7.9	–	UC after ME	0.292 ± 0.3-26	2091.4 ± 18-16.19	316.6 ± 398-.98	73 ± 13.9	3.6 ± 0.41	60.7 ± 6.8	
Ecological Park, Brazil (3° 43' S); São Francisco Zoo, Brazil (4° 21' S); Teresina Zoo botanical Park, Brazil (5º 05' S); Arruda Câmara Zoobotanical Park, Brazil (7º 06' S); and Dois Irmãos Park, Brazil (8º 03' S).	5 (captive)	70.8 ± 5.9	–	EE after DME	6.25 ± 2.7ml	142 ± 25.68	–	93 ± 1.5	4.8 ± 0.1	76.0 ± 3.5	Silva et al. (2019;[32])

[a] EE: electroeyaculation; EF: epididymal flush; UC: urethral catheterization; ME: medetomidine; DME: dexmedetomidine

Semen samples were also obtained and compared by Morato et al. (2001; [28]) from the six free-living and eight captive jaguars in the previously described study. Although, free-living male jaguars showed greater body weight and testicular volume, ejaculate volume was greater in captive jaguars. Free-living animals produced more, though non-significant, total spermatozoa, normal morphology, viability and forward progression (Table 2; [28]). In this study, the total proportion of structurally abnormal spermatozoa for the captive and free-living population ranged from 29.0% to 65.0% and 12.0–41.0%, respectively. Overall, for the captive jaguars, 30.0 ± 0.9% and 20.0 ± 0.9% of the total spermatozoa were classified as primary and secondary abnormal forms, respectively. There was a lower proportion of primary defects in the spermatozoa of the free-living population. In the captive group, primary abnormalities predominated, usually in the form of spermatozoa with malformed head shape or tightly coiled flagellum. In the free-living group, secondary abnormalities predominated, mainly as spermatozoa with a bent flagellum combined with a cytoplasmic droplet. The captive group showed greater proportions of microcephalic or bicephalic spermatozoa, or spermatozoa with a malformed head or acrosome, a tightly coiled flagellum, or a proximal or distal cytoplasmic droplet [28].

In a later study of this same group carried out in the Sao Paulo Zoo (Brazil, 23°39′3.2″ S) and the Sorocaba Zoo (Brazil, 23°30′21″S) two semen collections per animal were carried out by electroejaculation six months apart (January and July) in six males [29]. No difference was found between the first and second collections in any seminal trait, including volume, concentration, motility, forward progressive motility, and morphology. Seminal values of this study are included in Table 2 [29].

The most frequently found abnormalities in two samples obtained by electroejaculation in the study by Jimenez Gonzalez et al. (2017; [11]) were head defects, distal coiled tails, proximal coiled tails, detached heads, proximal cytoplasmic droplets and distal cytoplasmic droplets [11]. In the same study, seminal fluid obtained by epididymal flush in one male contained 35 ± 1.4% normal spermatozoids, the most frequent abnormalities found were distal cytoplasmic droplets, distal coiled tails, proximal coiled tails, proximal cytoplasmic droplets, detached heads, and head defects (Table 2; [11]).

In the study of Ribieiro de Araujo et al. (2018; [33]) semen samples from five wild (Taiamã Ecological Station 16°50'34.83"S, $n = 2$; Barranco Alto Farm 19°34'38.58"S, $n = 2$; and both in Pantanal and at the Serra da Capivara National Park in Caatinga 8°46'3.05"S, $n = 1$) and six captive (Mata Ciliar Association 23°10'41.30"S, $n = 2$; Paulínia Zoo 22°45'58.40"S, $n = 1$; and a non-governmental organization NEX 15°51'33.29"S, $n = 3$) jaguars were collected using medetomidine ketamine [33] for urethral catheterization. Forward progressive motility, sperm progressive motility, and sperm morphology analysis demonstrated the methodology did not adversely affect sperm quality [33]. Values are shown in Table 2.

In the study of Silva et al. (2019; [32]) semen was collected from 10 males by electroejaculation after dexmedetomidine administration. Two collections were performed per animal, with a minimum interval of 2 months between collections [32]. The greatest percentages of sperm defects were in the tail and head [32]. Spermatic values are shown in Table 2.

Mating

As jaguars are typically solitary animals, the male and female form temporary associations when they are ready to mate [18]. During the jaguar mating period, which can last from 9 to 20 days, males are attracted by olfactory and vocal signs emitted by females [34]. In the study by Jorge-Neto et al. (2018; [22]) in southern Pantanal of Brazil (16–20° S) male behavior showed two different sequences, characterized as copulatory behavior with or without penile penetration [22]. When no penile penetration occurred, the male left the female after finishing his pelvic movements [22]. When penile penetration occurred, which was the case in 42% of the mounts, this was followed by a sequence of female coital behavior [22].

This behavior was characterized by the female lying down in ventral decubitus with the hind limbs flexed under the body deviating the tail to one side and exposing the anal-genital region. Then, the male mounted the female approximating his genital region to the female's initiating pelvic impulses for penetration. Simultaneously, the male bit or licked the female's nape three or four times. The female emitted a low growling while the male roared indicating ejaculation. Finally, the female rocked – rolled into lateral dorsal decubitus [22] and both male and female began licking their genitals [20]. Similar to other felids, copulation occurs several times per day [2]. Male vocalization occurred nearly exclusively with penetration [22].

Finally, in a study carried out by Lanier and Dewsbury (1976; [35]) in the Rare Feline Breeding Center (Center Hill, USA, 28°37′19″ N) a couple of jaguars copulating was observed. The intromission duration was 2.3 ± 0.3 s and the inter-intromission interval was 55.25 ± 40.58 min [35]. Other authors reported the average length of copulation to be 2–9 s (range 2–35 s; [3]).

Discussion

This review summarizes the current knowledge on jaguar reproductive physiology identifying areas that need further research. The number of international peer reviewed original articles on the topic is surprisingly low. Furthermore, a limited number (mean six) of captive animals were used in most studies, and, therefore, are not fully representative of free - ranging populations.

Although the jaguar is approximately twenty-fold bigger than the domestic cat, both species show homologous reproductive anatomy [12,36]. As most felids, jaguars are reproductively classified as polyestrous and generally induced ovulators, with a moderate incidence of spontaneous ovulation [10,11,14]. As the proportion of induced ovulation has not been reported in this species yet, this parameter could not be compared among felids in which spontaneous ovulations can range from rare to occasional [13]. As shown in the domestic cat, in jaguars the percentage of spontaneous ovulation might be influenced by several male olfactory, visual and auditory sensorial stimuli [14,37,38].

As jaguars cover large geographical areas, several reproductive patterns have been described. In the Equatorial and Tropical zones, where no light differences are present among the seasons, jaguars may breed throughout the year. Thus, as some jaguars were located in intertropical areas [6,11,32], seasonality could not be manifested. The effect of local rains has been found to be relevant [11] with mating increasing when floodwaters recede. However, the true stimulus is likely to be the availability to prey and not rainfall itself [39]. Thus, the fact that the increased frequency of jaguar births coincides with the dry season seems to be an evolutionary strategy to take advantage of increased food availability for growing litters during lactation [39]. Conversely, there is evidence of seasonality in Temperate zones with births occurring mostly in summer and spring months [18]. Furthermore, in the domestic cat the feasibility of seasonal anestrus is nil up to 35° latitude, where there is only a diminution of reproductive activity during months with decreasing photoperiod [40,41]. A similar reproductive seasonal pattern could be expected in jaguars.

Puberty is reasonably stable across Felidae with smaller species attaining sexual maturity at an earlier age − 1year old or less - than larger species − 2 years - [19]. Although descriptions of pubertal transitions in jaguars are extremely scarce, sexual maturity was reported to occur at about two years of age [18]. Specifically, only two studies described puberty achievement in four captive jaguars around the Tropical areas [12,19]. As age at puberty was greater (19 vs. 29.5 months) in the study in which only behavior was assessed, it could have been possible that previous pubertal silent cycles were not detected [12]. No information about the body weight at puberty has been

reported in jaguars. Assuming jaguars achieve puberty at 75–80% adult body weight, depending on the geographical population, puberty could be expected at approximately 59 kg and 44 kg in males and females, respectively.

The standard ovarian steroid hormone pattern in felids is characterized by estrous cycle of two to four weeks-, with estrus lasting three to 10 days [42]. When compared to the domestic cat, the jaguar estrous cycle is characterized by a longer duration of its phases. Considerable variation in jaguar estrus and estrous cycle lengths was found, with means and ranges of 9.45 days (4 − 17) and 39.11 days (22 − 63), respectively. These variations could be attributed to the scarce number of animals included, the different geographical locations and to the dissimilar methods (i.e. behavior vs. hormonal) used to identify these periods. Accordingly, hormone monitoring might provide a more reliable indicator of estrus than observations of behavior [10].

In other Panthera species, length of the non-pregnant luteal phase – pseudopregnancy – is about one-half to two thirds that of pregnancy [13]. Similarly, reports in jaguars based on hormonal determinations reported, a range of 14–67 days for pseudopregnancy periods [10,11]. Coincidentally, in domestic cat, pregnant and non-pregnant luteal phase last approximately 65 days and 40 days, respectively [38].

Mean gestation length for the jaguar is similar to those of the other members of the Panthera genus (91–110 d) [10]. Gestation length in mammals is largely accounted for by differences in body size. Correlation between body weight and gestation length [24] in 11 feline species was 0.81. Thus, this coefficient supports the hypothesis that larger cats have longer gestation periods.

As previously explained, progestins have a rather restricted application for pregnancy diagnosis in felids. Although it requires general anesthesia, ultrasonography is the most frequently used method to diagnose pregnancy in wild felids. Litter size and a rapid post-partum estrus resumption for jaguars are also in line with most Felidae.

As described in this review, controversial findings were reported when assessing male seasonality. Latitudinal placement of the different male studies should be considered since it clearly influences the reproductive findings. Although, testosterone metabolite levels are expected to increase during the mating season, which is consistent with the role of testosterone on spermatogenesis [17]. In an initial report in male jaguars, this hormone did not vary throughout the year [43]. Thus, it appears that reproductive seasonality in male jaguars is moderate to none. Further work should be carried out in larger number of males, using standardized immunomethods to unveil the effects of light and rain at different geographical areas.

Compared with mammalian species, the gonadosomatic index found for jaguar is quite low, almost 40% smaller than that for domestic cats [26,31,44]. This latter finding was quite expected as in mammals, the relative size of testes is inversely proportional to body size [27].

The total duration of spermatogenesis in jaguar is ~ 25% longer than that found for the domestic cat [26,45]. When working with jaguar semen the ten-day difference in spermatogenesis should be borne in mind. The percentage of testis occupied by seminiferous tubules in jaguars is also 10% smaller than in the domestic cat [27] being in the lowest physiological range described for mammals [30]. Although, in jaguars the length of seminiferous tubule per gram of testis is within the range of most domestic animals [30], this value is also below of that described for the domestic cat [45].

The jaguar has smaller volumetric proportion of seminiferous tubules, shorter seminiferous tubule length per gram of testis and proportionally smaller testes than the domestic cat. However, as there is a lower loss during spermatogonial mitoses and meiotic divisions (30% vs. 20% in the jaguar; [31]), and Sertoli cells have a higher capacity for supporting round spermatids. Thus, the whole process of sperm production of jaguars is more efficient than the cat [27]; but is low in relation to most of domestic animals (37.4–74.2 round spermatids; [30]) [27].

The number of Leydig cell per gram of testis is approximately threefold higher than in domestic cats [27]. Nevertheless, the reason for the high percentage occupied by these cells in jaguar testes is not known and correlation with higher testosterone concentrations has not been found [27].

Comparisons among reports on jaguar seminal evaluation are difficult as findings are, in general, quite variable. Although seminal volume was higher in the four studies in which collection was carried out by electroejaculation [11,28,29,32], total count and spermatozoa concentration were higher in the report using urethral catheterization after medetomidine [33]. In the study of Silva et al. (2019 [32]) in which dexmedetomidine was used before to the electroejaculation, average sperm concentration was high compared to values reported in previous studies. The increase in sperm concentration was due to the improvement in ejaculation potential induced by medetomidine, which appears to be the most efficient option examined to date [32]. Although reproductive seasonality may also influence semen quality [26] all the seminal studies were carried out within the Equatorial or Tropical areas and, therefore, no differences were found [29].

Electronic microscopy revealed that in jaguars, as in other Pantherinae species, sperm tends to have a more rounded morphology than the domestic cat, with the total spermatozoa length being similar [32].

Normal morphology (64.57 ± 12.06%) and motility (81.75 ± 8.30%) was found in most studies on jaguar semen. Thus, jaguars have been generally considered normospermic (~65% normal) [18]. This low percentage of morphological abnormalities contrasts with high values of pleiomorphisms found in other felid species [11]. Poor semen quality presented in felids is usually associated with low genetic diversity. Accordingly, based on sperm quality, maintenance of the currently acceptable level of genetic diversity should be a long-term goal for all jaguar conservation management programs. Impaired spermatogenesis due to suppression on the gonadal axis of males in captivity has been described [46].

In spite of few reports, it seems that the general sequence of copulation-related behavior in jaguars resembled those of the domestic cat and other Felidae species [3]. Although, domestic cats are reported to assume a neck grip and to tread prior to extra-vaginal thrusting and insertion, large Felidae do so only after intromission has been achieved [35]. The elevated copulation frequency in jaguars could be partly explained according to Jorge-Neto et al. (2018; [22]) by the fact that penile penetration occurred in less than the half of the mountings.

Final conclusions

As expected, jaguar reproduction patters are similar those of other large felids [27,44,47]. Although the domestic cat can be used as an experimental model for jaguars, species reproductive physiological differences should be borne in mind. As evidenced by the wide range reported for most reproductive parameters further work on larger sample sizes is necessary to explain causes of variability and to achieve fundamental knowledge of key aspects of reproductive biology in this threatened species that could facilitate breeding, management and conservation activities.

Conflict of interest

The authors do not have any financial nor personal relationships with other people or organizations that could inappropriately influence the study.

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