


REVIEW ARTICLE

Reproductive physiology with emphasis on endometrial cycles of woolly and uakari monkeys—A literature review

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Abstract

The ability of a species to withstand human impact depends on its life history characteristics, including social, ranging, and reproductive activity. The genera *Lagothrix* and *Cacajao* are more susceptible to anthropic action than small-sized primates due to their slower life histories, more restricted geographical ranges, and lower population densities. This narrative literature review aimed to gather scientific information available from the last 60 years on the reproductive biology of females of the genera *Lagothrix* and *Cacajao*. Most studies on the genus *Lagothrix*, mainly focused on *L. lagothricha* and *L. l. poeppigii*, present important advances on reproductive strategies, reproductive productivity, functional morphology and physiology, including seasonality, sexual cycle, gestation and fetal development in captive and free-living populations. Contrary, there is much less known about the reproductive biology of the genus *Cacajao*, with studies on free-living *C. calvus* and *C. melanocephalus* highlighting reproductive behavior, and basic description of the sexual cycle, gestation, and lactation. Unfortunately, the morphology of the female genital organs is only described in *C. calvus*, and there is still scarce information about the menstrual activity and the placenta. This literature review encourages primatologists, morphophysiologicals, reproductive specialists, and ecologists to conduct comprehensive studies of these species to better understand the gaps in

Abbreviations: ARTs, assisted reproductive technologies.; CAPES, coordination for the improvement of higher education personnel.; CL, corpus luteum.; CNPq, National Council of Technological and Scientific Development.; PROCAD, National Academic Cooperation Program in the Amazon.

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knowledge about reproduction, their relationship with their environment, including climatic and social variables. Understanding the integrative reproductive biology of these species will be a clue for improving the assessment of the resilience capacity of free-living populations and, consequently, establishing more appropriate management programs, and for the development of ex situ management techniques for the conservation of the species.

KEYWORDS

genital morphophysiology, new world primates, reproductive cycle

1 | INTRODUCTION

Habitat destruction, predatory hunting, and climate change hinder wildlife maintenance and promote species extinction (Sutherland et al., 2021). Although there are variations in the specific characteristics of the adaptability of species to human action, the common responses observed are population decline and short-term extinction (Estrada et al., 2018). Understanding the reproductive biology of wild species helps assess the responses of wild populations to different levels of depredation and, thus, sustainability of their populations in the wild (Bowler et al., 2014; Mayor et al., 2017).

Regarding Neotropical nonhuman primates, research has traditionally been based only on systematic observations of social and reproductive behavior, which limits the acquisition of information related to morphophysiological aspects (Andrabi & Maxwell, 2007; Pukazhenthi & Wildt, 2004). Although studies on endocrinology and reproductive cycles are available, they are specifically focused on species raised in animal facilities and used as experimental models (Bakker et al., 2018; Fernandez-Duque, 2012; Lima et al., 2019). However, the maintenance of wild species in captivity can produce important reproductive variations due to multiple factors, such as stress, availability of resources, territories, and the composition of social groups (Mayor et al., 2017). Previous research has described different presentations of the sexual cycle depending on the primate species; while the menstrual cycle has been identified in *Alouatta guariba clamitans* (Silvestre et al., 2017) and genera *Aotus*, *Cebus* and *Sapajus* (de Lima Cardoso et al., 2021; Mayor et al., 2019), *Callithrix* (Abbott, 1992) and *Saimiri* (Srivastava et al., 1970) have estrous cycles. However, reproductive knowledge is still absent for many medium- and large-sized primates, such as woolly monkeys (genus *Lagothrix*) and uakaris (genus *Cacajao*). For instance, preliminary studies suggested nonmenstruating cycles in the Poepig's woolly monkey (Mayor et al., 2012) and the red uakari (Mayor et al., 2013a; Mayor et al., 2019).

Woolly and uakari monkeys are frequently hunted for self-consumption of meat and the pet trade of juveniles (Aquino et al., 2022; Bowler et al., 2014; Mayor et al., 2017). Furthermore, their slow life history and low tolerance for habitat degradation promotes these primates to have greater difficulty replenishing their populations in the wild and a restricted distribution compared to other primate species (Aquino et al., 2022; Ellis et al., 2021; Mooney

& Lee, 1999). The anthropogenic impact on these genera is reflected in the IUCN Red List, where woolly monkeys are classified as Critically Endangered (*L. flavicauda* and *L. lugens*), Endangered (*L. cana* and *L. l. poeppigii*), and Vulnerable (*L. lagothricha*) species (Cornejo et al., 2021; Shanee et al., 2021a, 2021b; Stevenson et al., 2021a, 2021b). The subspecies *L. tschudii* is listed as Data-Deficient because of limited research (Vermeer et al., 2021). Uakari monkeys are classified as Vulnerable (*C. calvus* and *C. homosi*) and Least Concern (*C. ayresi* and *C. melanocephalus*) species (Aquino et al., 2022; Boubli et al., 2021a, 2021b; Mittermeier et al., 2021).

Captive breeding can also be important to provide knowledge that may be useful due to the availability of populations. The reproductive information from captive populations can contribute to improving conservation strategies, especially in species that have not been well studied in the wild; but reproductive data are still scarce, particularly when captive populations are difficult to breed in captivity (Mayor et al., 2017). Thus, it is essential to improve our knowledge of the reproductive physiology of these species to advance their management and develop conservation strategies to prevent population declines (Mayor & Bowler, 2015; Mayor et al., 2012, 2013b, 2019).

This review of the scientific production contributes to gathering relevant information in an orderly and comprehensive manner, summarizing the current knowledge regarding the reproductive biology of the genera *Lagothrix* and *Cacajao*, covering the biological characteristics and reproductive morphophysiology of females. By identifying gaps in knowledge about the reproductive biology of both species, we aim to encourage primatologists, morphophysiologicals, reproductive specialists, and ecologists to develop future and integrative studies to advance knowledge of the field, as well as for the development and application in situ and ex situ of reproductive biotechniques and conservation techniques.

2 | DATABASE SEARCH AND SOURCE IDENTIFICATION

The search of scientific literature was conducted with a focus on articles published in the last 60 years (1963–2023) using the bibliographic databases SciELO, PubMed, and Google Scholar with

the following keywords: reproductive cycles, morphophysiology, female reproduction, menstruation, *Lagothrix*, and *Cacajao*. A total of 2040 references (journal articles, books, books, chapters, dissertations, monographs, and webpages) were identified, initially based on the title, then refined by the abstract, and finally read in full. After the removal of duplicates, applying inclusion and exclusion criteria and necessary variants, 39 articles, 7 books, 4 book chapters, 3 dissertations, 1 monography, and 10 webpages remained for analysis. In addition, articles with an emphasis on publications in international journals containing the most recent information (2017–2023), and older publications with unprecedented and highly relevant information on topic and reference books were also included in the review.

We conducted a literature review to address the biological characteristics of the genera and describe the morphophysiology of the female reproductive system, with an emphasis on differences between estrous and menstrual cycles, and endometrial changes throughout the reproductive cycle.

3 | WOOLLY MONKEYS

3.1 | Biological characteristics

Woolly monkeys (genus *Lagothrix*) are members of the family Atelidae together with howler monkeys (*Alouatta* spp.), belong to the subfamily Atelinae along with spider monkeys (*Ateles* spp.) and woolly spider monkeys (*Bachyteles* spp.) (Groves, 2005). They are large-bodied primates weighing approximately 6 and 10 kg with thick woolly fur and prehensile tails (Ford & Davis, 1992; Levi & Peres, 2013). In contrast to other genera of the Atelinae subfamily, sexual dimorphism has been observed in adult animals, with adult females and males weighing on average 6 and 8 kg, respectively (Di Fiore et al., 2014; Peres, 1994; Ramirez, 1980). Heavier adult males have more developed secondary sexual characteristics than lighter males, and their upper canines are longer than those of females (Di Fiore et al., 2014; Fooden, 1963).

Woolly monkeys are widely distributed in the Central and Western Amazon (Figure 1a), with species distribution varying in more restricted or dispersed areas in different countries (Di Fiore et al., 2015; Fooden, 1963). *Lagothrix flavicauda* (yellow-tailed woolly monkey) is endemic to Peruvian forests (Shanee et al., 2021a), whereas *L. lagothricha* (common woolly monkey) has an extensive distribution range that includes Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela (Stevenson et al., 2021a). *L. l. poeppigii* (Poeppigii woolly monkey) occurs in the primary forests of Brazil, Ecuador, and Peru (Shanee et al., 2021b), and *L. cana* (Geoffroy's woolly monkey) is present in forests of diverse states of Brazil and in the region of Peru on the border with Bolivia (Cornejo et al., 2021). In contrast, *L. lugens* (Colombian woolly monkey) has a restricted distribution and isolated populations are present along the Central and Oriental Andean cordilleras and forests of Colombia (Stevenson et al., 2021b). It is also estimated that *L. tschudii* (Tschudi woolly monkey) has a localized

distribution in Peru and Bolivia at higher altitude, although its exact range is not known (Vermeer et al., 2021).

Woolly monkeys live in heterosexual groups of 12–40 individuals, forming subgroups that maintain auditory contact (Defler, 1989). In the wild, woolly monkeys have a diet based mainly on fruits, but leaves and arthropods also are included, especially in the diets of infants and nonpregnant females (Jesus et al., 2022; Stevenson et al., 1994; Torres et al., 2022). The ingestion of arthropods reduces conflict in the group during periods with lower fruit availability, because juveniles and nonlactating females feed on more insects, while dominant males and lactating females ingest fruits (Stevenson et al., 1994).

3.2 | Female reproductive morphophysiology

The macroscopic morphology of the female genital organs of the *L. l. poeppigii* is similar to that in other primates (Figure 2a). The ovaries are creamy-white with an ovoid shape and smooth surface. Pregnant females have larger ovaries than nonpregnant females and no difference has been observed between the right and left ovaries (Mayor et al., 2013b). The tunica albuginea is formed by dense connective tissue that lines the cortical region where the ovarian follicles and corpus luteum (CL) are located. Due to follicular selection, only one or two ovarian follicles develop and reach preovulatory follicular diameter between 0.5 and 1.0 cm. Only preovulatory follicles were visible as transparent bodies but did not protrude above the surface (Mayor et al., 2013b). Pregnant and luteal phase females had CL invading the entire ovarian stroma (Figure 2b). Some nonovulated follicles do not undergo atretic processes and transform into accessory CL which can increase progesterone secretory activity (Mayor et al., 2013b).

The uterine tubes of woolly monkeys are simple, approximately 6 mm long, without a sphincter in the uterotubal junction or protruding papilla. There is no formation of ovarian bursa by mesosalpinx, which increases the possibility of the migration of oocytes into peritoneal cavity when compared with species that have a complete ovarian bursa (Mayor et al., 2012). Microscopically, the infundibulum has a more ciliated epithelium, thinner muscular layer, and larger lumen when compared with the other portions of uterine tubes (Mayor et al., 2012). The number of ciliated and secretory cells in the uterine tube varies according to the reproductive cycle, with greater development of the ciliated epithelium observed in the follicular phase, whereas secretory cells are predominant in the luteal phase and gestation (Mayor et al., 2012).

The uterus of woolly monkeys is an elongated organ consisting of a single cavity with a globular fundus and a long cervix (Mayor & López-Plana, 2021; Mayor et al., 2012; Figure 3). In nonpregnant females, the uterus is completely located in the pelvic cavity and has an average length of 2.9 cm in the proliferative phase and 3.2 cm in the secretory phase; in pregnant females, the uterus undergoes an important growth that extends into the abdominal cavity. The myometrium contains two concentric layers of smooth muscle with

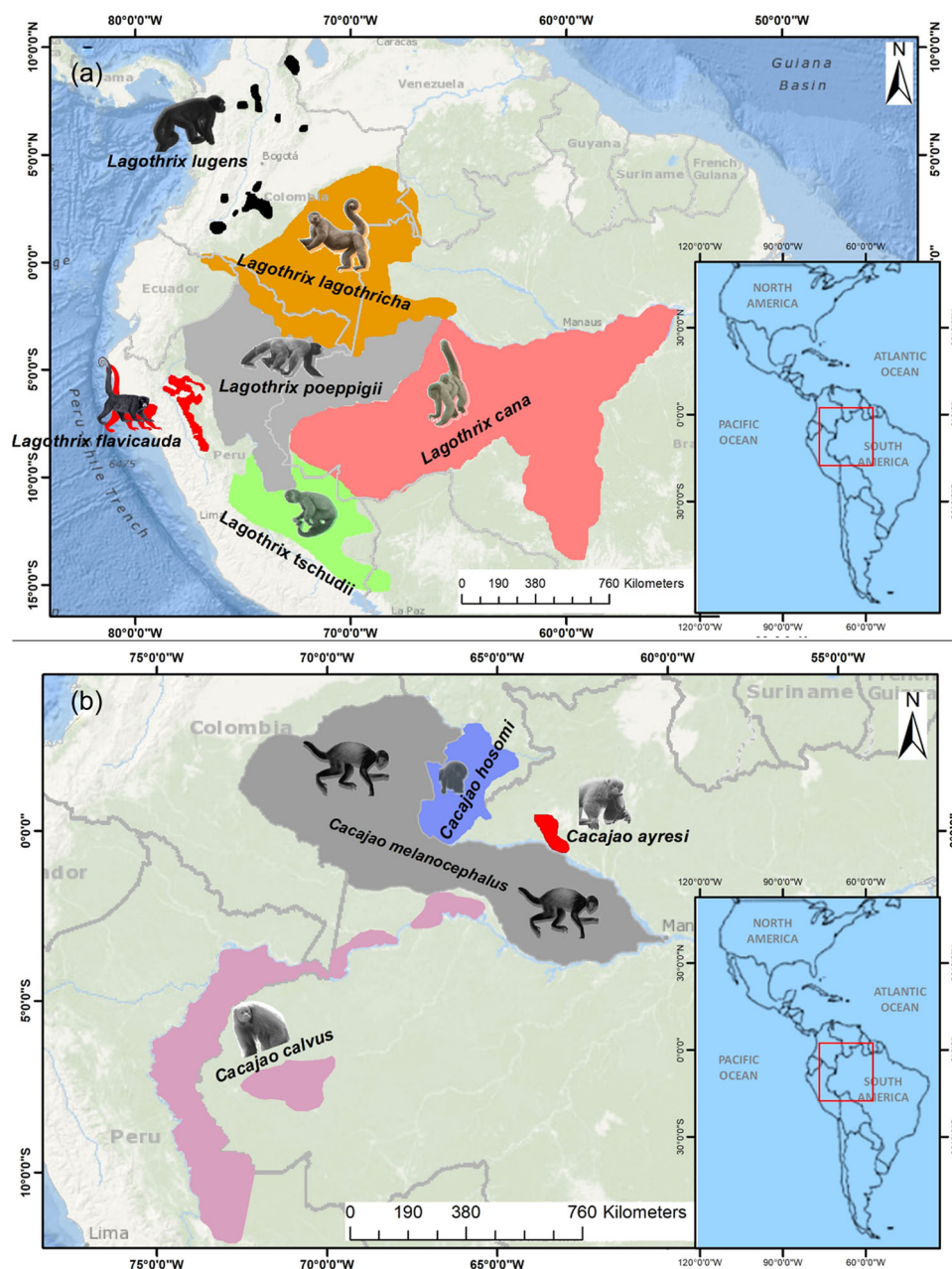


FIGURE 1 Geographic distribution of six woolly monkey species (a, genus *Lagothrix*) and four uakari monkeys (b, genus *Cacajao*). They are distributed from Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. Source: adapted by Biologist Nelton Luz from Aquino et al. (2022), Boubli et al., (2021a, 2021b), Cornejo et al. (2021), Mittermeier et al. (2021), Shanee et al., (2021a, 2021b), Stevenson et al., (2021a, 2021b), and Vermeer et al. (2021).

circular inner and longitudinal outer layers. Between both muscular layers, a vascular layer is formed by the uterine arteries that, upon reaching the endometrium, divide into straight and spiral arteries (Mayor et al., 2012).

The endometrium is composed of invaginations in the stroma and extensions of columnar epithelial cells responsible for the formation of simple coiled tubular glands. In the early follicular phase, the females present a thin endometrium with moderate vascularization and a high quantity of collagen under the epithelium. Along the growth of antral follicles, the endometrium undergoes tissue remodeling and extensive

proliferation to develop the epithelium and stroma, becoming richly vascularized. In addition, after ovulation, straight tubular glands proliferate and initiate secretory activity (Mayor et al., 2012). In the luteal phase, the females have thickening of the myometrium and endometrium with increased vascularization and proliferation of branched glands, transforming the endometrium from proliferative to secretory type and preparing to host a possible gestation (Figure 4a–c). During gestation, the uterine body expands, the endometrium and the myometrium become thinner, and endometrial glands are not often observed (Mayor & López-Plana, 2021).

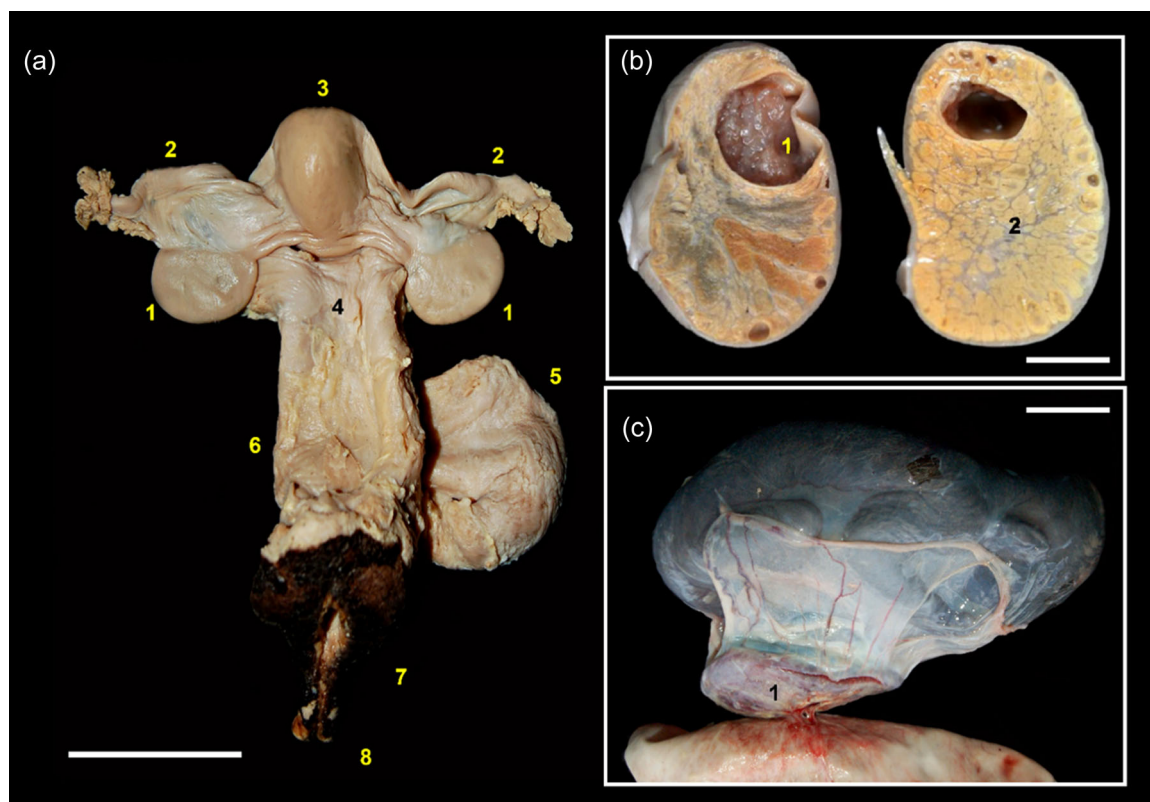


FIGURE 2 Genital organs of female Poeppig's woolly monkeys (*Lagothrix poeppigii*) in different stages of reproductive cycle; (a) Dorsal view of the genital organs in early follicular phase: 1. Ovaries; 2. Uterine tubes; 3. Uterine body; 4. Cervix; 5. Urinary bladder; 6. Vagina; 7. Vulva; 8. Clitoris. (bar: 2 cm). (b) Sections of ovaries in follicular phase (left) and luteal phase (right): 1. Preovulatory follicle; 2. Gestational CL with antral cavity (bar: 0.25 cm). (c) Fetal membranes and fetus in intermediate gestational period. The placenta is discoidal, deciduous, and hemochorial: 1. Maternal-fetal contact discoid zone (bar: 2 cm). Source: adapted from Mayor and López-Plana (2021).

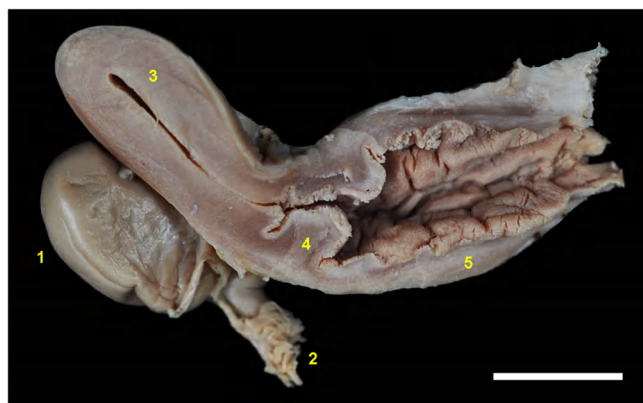


FIGURE 3 Longitudinal section of the genital organs of a female woolly monkey (*Lagothrix poeppigii*) in early follicular phase. 1. Ovary; 2. Uterine tube (infundibulum); 3. Uterine body; 4. Cervix; 5. Vagina. (bar: 0.5 cm). Source: adapted from Mayor and López-Plana (2021).

In the absence of fertilization, the uterus releases prostaglandins and promotes CL regression, which causes a reduction in progesterone levels. As a result, arterial constriction occurs in the endometrium and the release of enzymes responsible for local necrosis and rupture of the extracellular matrix, respectively. Large amounts of collagen in

the early follicular phase indicate local remodeling following the degradation of the functional layer (Critchley et al., 2020; Mayor et al., 2012).

Mayor et al. (2012) reported that the endometrium in the female woolly monkey has characteristics similar to those of primates with menstrual cycles, with spiral arteries in the endometrium and a high amount of collagen in the initial proliferative phase. Fibrin clusters were also observed during early follicular growth; however, detachment of the functional layer or bleeding was not observed, which did not allow characterization of the menstrual cycle (Mayor et al., 2019; Figure 4d).

In women and macaques (genus *Macaca*), the reduction of progesterone by luteolysis causes contraction of spiral arteries located in the functional layer of the endometrium (Critchley et al., 2020; Reavey et al., 2018). Thus, blood flow is blocked; it causes ischemia in the region responsible for the necrosis of the endothelium and apoptosis of the epithelial cells in the functional layer. With the disruption of local vascularization, clots are formed mixed with the desquamated endometrium that are eliminated and constitute the visible sign of menstruation. Thus, at the end of menstruation, the endometrium shed and reduces to a very thin basal layer with the ability to fully regenerate, allowing the development of a next menstrual cycle (Critchley et al., 2020; Slayden & Calhoun, 2018).

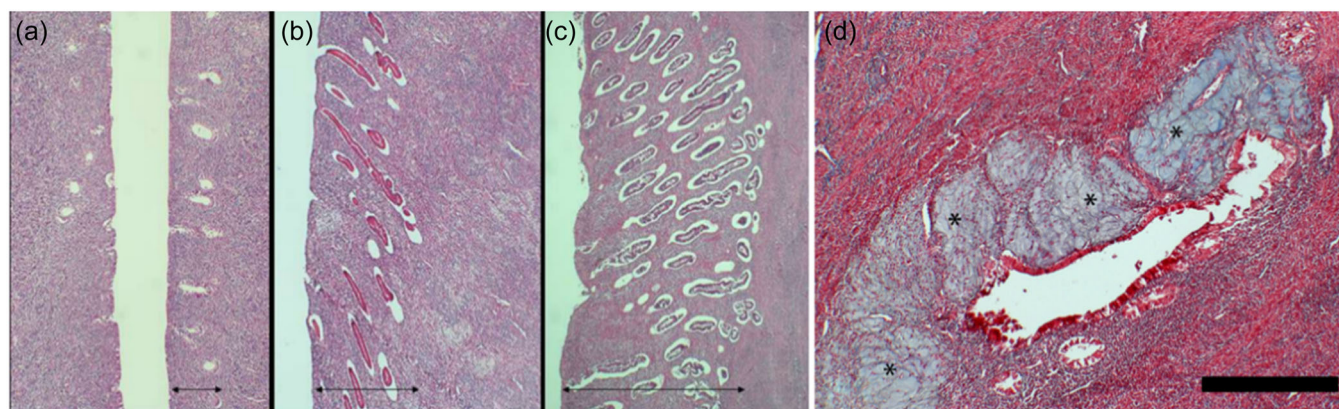


FIGURE 4 Photomicrographs of the uterine body of a nonpregnant female woolly monkey (*Lagothrix poeppigii*) demonstrating the progressive growth of the endometrium and endometrial glands: (a) Early follicular-proliferative phase, (b) Intermediate follicular-proliferative phase, and (c) luteal-secretory phase of the estrous cycle. H&E; (d) Uterine body with fibrin clots (*). Masson's trichrome (bar: 0.5 mm). Source: a–c: Mayor and López-Plana (2021); d: Mayor et al. (2019). H&E, hematoxylin and eosin.

Initially, Old World primates were considered menstrual cycle species, whereas New World primates had estrous cycle because macroscopic features of endometrial bleeding were not observed (Blaffer & Whitten, 1987). However, according to Pereira et al. (2020), endometrial features associated with the menstrual cycle have been also reported in Atelidae. The brown howler monkey (*Alouatta guariba*) exhibits areas of desquamation on the surface of the uterine epithelium, erythrocytes in the lumen of the endometrial glands, and subepithelial blood leakage; however, no cilia or microvilli in the epithelial cells or macroscopic bleeding were observed (Pereira et al., 2020). Kaiser (1947) evaluated the uterus of the mantled howler (*Alouatta palliata*) and did not observe spiral or analogous arteries in the endometrium. Contrary, other studies report the presence of erythrocytes in the vaginal lumen at the end of the luteal phase, suggesting that this species has a menstrual cycle (Kugelmeier et al., 2011; Silvestre et al., 2017). Similar features were reported in the Geoffroy's spider monkey (*Ateles geoffroyi*), spiral arteries were also absent in the endometrium and there was mild bleeding with a small number of erythrocytes in the vaginal lumen, suggesting micromenstruation (Hernández-López et al., 1998).

The cervix has primary folds in the mucosa and secretory cells included in the monolayer and columnar epithelium. Pregnant females present a larger proportion of cervical secretory cells and mucous secretions in the lumen than nonpregnant females (Mayor & López-Plana, 2021, Figure 3). Under the influence of progesterone, the cervical mucus closes the canal so that foreign material cannot enter the uterus during gestation (Senger, 2005). In females in the estrous phase, increased vascularization and rising levels of estrogens promote fluid secretion, permitting the passage of spermatozoa into the uterus (Lyngset, 1968).

The vaginal mucosa in the *L. l. poeppigii* has a stratified squamous epithelium, well-developed cornification, and various papillae in the lamina propria. During the reproductive phase, the vaginal epithelium shows changes in thickness, number of cell layers, and cornification. Females in the follicular phase show a clear pattern of cornification,

and hypertrophy and cornification of the vaginal epithelium related to the follicular development. Females in the luteal phase maintain the epithelium thickness but lose the epithelial cornification. Finally, during the gestational period, the vaginal epithelium becomes thinner and noncornified (Mayor et al., 2012). These vaginal features suggest that vaginal cytology could be a successful methodology to characterize the estrous cycle.

Regarding the placenta, the woolly monkey has a hemochorial and deciduous placenta similar to that of other primates, including humans. In contrast to most platyrrhine primates that present only one maternal-fetal attachment, this species presents a discoid placenta with one region of maternal-fetal attachment, although a bidiscoid placenta is also observed in a lesser proportion (Figure 2c) (Mayor & López-Plana, 2021; Mayor et al., 2012). Phylogenetic analysis of primates suggests that the bidiscoid placenta is a posterior evolution in the placentation of large-bodied Neotropical monkeys (genera *Lagothrix* and *Alouatta*) (Wildman et al., 2006). The allantois is a simple elongated oval sac located next to the yolk sac and extends to the surface of the placental disc between the amnion and the chorionic plate. The insertion of the umbilical cord in the placental disc of *L. lagothricha* is marginal, while it is velamentous in *L. cana* (Young, 1972).

3.3 | Reproductive biology

The reproductive biology of the woolly monkey is similar to that of other Atelids primates in many aspects, except for the immigration process and age at first mating. Groups of woolly monkeys are characterized by male philopatry, whereas females leave their native groups (Di Fiore et al., 2009; Stevenson et al., 1994; Stevenson, 2002). Juvenile females remain in the birth group until the start of reproductive activity at approximately 6 years of age; after reaching sexual maturity, nulliparous females leave their native group and migrate to other groups (Nishimura, 2003; Schmitt, 2010).

Males and females mate with multiple members of the opposite sex, forming polygynandrous mating systems (Mack & Kafka, 1978; Nishimura, 2003). Free-ranging females exhibit sexual behavior toward males before leaving their native groups (Di Fiore et al., 2009). Migration to other groups usually occurs when females are in the estrous phase, and are likely to accept males from other groups. Females do not show visible signs of estrus, which makes it difficult to identify the conception date (Di Fiore et al., 2011). In captivity, mature males and females of *L. lagothericha* rarely interact, and it is common for them to engage in individual activities. When females are in estrus, mature males follow them and smell their anogenital region. Inactive females either do not assume a mating position or prevent complete copulation. Adult males can copulate with each receptive female of the group during the estrous period (Mack & Kafka, 1978).

In the Peruvian Amazon, births occurs between March and August, whereas the conception periods are concentrated in July and January. *L. l. poeppigii* shows seasonal reproductive patterns in the wild and can be observed even in reduced populations owing to climate and food availability (Mayor et al., 2017). This seasonality is similar to that observed in groups of wildlife primates located in a primary rainforest in Ecuador, with conceptions between September and January and births concentrated in May and September (Ellis et al., 2021). In tropical forests, the reproductive activity of woolly monkeys appears to be opportunist seasonal breeders capable of breeding year-around when sufficient food is available (Bowler et al., 2014). In contrast, in captivity, Mooney and Lee (1999) observed females giving birth throughout the year, which was probably related to a constant food supply.

Scientific information on reproductive biology is only based on *L. lagothericha* and *L. l. poeppigii*. These species have a long-life history compared to other primates of similar body mass, as evidenced by the late age at first reproduction and long interbirth intervals (Di Fiore et al., 2011; Mooney & Lee, 1999; Nishimura, 2003; Table 1). In the wild, the female woolly monkey reach sexual maturity at approximately 6 years of age when they begin their reproductive activity (Nishimura, 2003). Similar results were observed by Mooney and Lee (1999) when evaluating the reproductive parameters from different captive populations; they observed that females start reproducing at a late age, with a median age at first birth of 6–7 years and a short duration of total reproductive period (4–5 years). Females born in captivity were younger at first reproduction than wild-caught females (median: 6.2 vs. 9.0 years, respectively) and showed shorter interbirth intervals (median: 25 vs. 30 months). Contrary, Timmer (2006) reported that captive females have a shorter reproductive lifespan of 13 years, reaching reproductive maturity later than free-living females (6–7 vs. 4–5 years).

The female woolly monkey has an estrous cycle of 21–25 days, with an estrus of 1–8 days (Abondano et al., 2022; Castellanos & Louis McCombs, 1968; Mack & Kafka, 1978; Williams, 1967), being receptive to copulation and accepting males, with an interval of 3 weeks.

In the wild, the average age at first parturition is 9 years and the gestation period varies from 214 to 228 days (Nishimura, 2003). Females do not return to sexual activity until 20 months after parturition resulting in an average inter-birth interval between 30 and 37 months, and 0.29 births per year and female (Ellis et al., 2021; Mack & Kafka, 1978; Mayor et al., 2017; Mooney & Lee, 1999; Nishimura, 2003; Robinson & Redford, 1986; Williams, 1967).

In the wild, the female woolly monkey usually delivers at term one infant (De Andrade et al., 2018; Mayor et al., 2017; Nowak, 1999; Ross, 1988, 1991); however, in captivity, a particular case of three youngs has been recorded (Mooney & Lee, 1999). In wild populations in the Peruvian Amazon, Bowler et al. (2014) observed an average ovulation rate of 1.74 CL per female, but all pregnant females had a single pregnancy, with a fetal sex ratio of 1:1. These wild populations have an annual reproductive production of 0.48–0.54 newborns per pregnant female, resulting in an interbirth interval between 22 and 25 months (Bowler et al., 2014).

Neonates are born with approximately 10% of the maternal mass (Mack & Kafka, 1978) and present high levels of altriciality, since the covering pelage are not fully developed, and they do not have open eyelids or tooth eruption (De Andrade et al., 2018). Thus, *L. l. poeppigii* give birth to highly altricial, fully dependent on a long parental care, in terms of thermal regulation, motility, and feeding. At the end of pregnancy, fetuses they cannot ingest solid food until the 11th postnatal week, resulting in delayed weaning ranging from 18 to 24 months (Mack & Kafka, 1978). The extended parental care from the postnatal period until the young becomes independent implies a slower postnatal growth and a higher maternal energy, increasing the interval between deliveries and decreasing reproductive rates (De Andrade et al., 2018).

4 | UAKARI MONKEYS

4.1 | Biological characteristics

The uakaris are Neotropical primates belonging to the genus *Cacajao* and comprise the subfamily *Pitheciinae* along with sakis (genus *Pithecia*) and bearded sakis (genus *Choropotes*) (Groves, 2005). They are medium-sized primates, weighing between 2.3 and 4.5 kg (Mittermeier et al., 2013) and body length variation from 30 to 50 cm (*Cacajao melanocephalus*) or 36 to 57 cm (*C. calvus*), and with nonprehensile tails shorter than their body (Barnett et al., 2013; Mittermeier et al., 2013). The species *C. melanocephalus*, *C. homosi*, and *C. ayresii* have naked and black faces, whereas *C. calvus* is characterized by the absence of fur on its head and by a crimson red face (Barnett & Brandon-Jones, 1997; Hershkovitz, 1987). Sexual dimorphism has been observed in these species, with males being slightly larger and heavier than females (Barnett et al., 2013). Generally, uakari monkeys form multimale-multifemale groups of varying sizes because of the fission-fusion behavior observed in these species (Barnett et al., 2013; Bowler & Bodmer, 2009; Di Fiore &

TABLE 1 Physical characteristics and female reproductive parameters in woolly monkey (genus *Lagothrix*) and uakari monkey (genus *Cacajao*).

Species	Physical characteristics			Female reproductive parameters							
	Head-body length (cm)	Tail length (cm)	Weight (Kg)	References	Sexual maturity (years)	Cycle (days)	Gestation (days)	Birth interval (months)	Offspring per gestation	Breeding condition	References
<i>Lagothrix lagotricha</i>	46–65 (males)	53–77 (males)	7.0–10.0 (males)	Mittermeier et al. (2013)	-	21	228.1	9–12	-	captive	Williams (1967)
					-	23–26	-	-	-	captive	Castellanos and Louis McCombs (1968)
					-	17–26	225	12–24	-	captive	Mack and Kafka (1978)
	46–58 (females)	62–72 (females)	5.0–7.0 (females)		6	23–26	223–225	36.7	1–2	wild/captive	Mittermeier et al. (2013)
					6–7	-	-	22	1	wild	Mooney and Lee (1999)
					6	-	213–228	36.7	-	wild	Nishimura (2003)
<i>Lagothrix poeppigii</i>	46–65 (males)	62–80 (males)	7.0–10.0 (males)	Mittermeier et al. (2013)	-	-	-	22.3–25.2	-	wild	Bowler et al. (2014)
					-	22.9	220	36.7	-	wild	Ellis et al. (2021)
	46–58 (females)	53–72 (females)	5.0–7.0 (females)		-	21.9	214	36.7	-	wild	Abondano et al. (2022)
					-	-	225	-	1	wild	Mittermeier et al. (2013)
<i>Cacajao calvus</i>	38–56 (males)	14–19 (males)	3.0–3.5 (males)	Mittermeier et al. (2013)	-	-	180	-	1	wild	Ayres (1989)
					-	-	-	24	-	wild/captive	Fontaine (1981)
	36–57 (females)	14–17 (females)	2.3–3.0 (females)		-	-	190	-	1	wild	Mittermeier et al. (2013)
					3.5	14–42	-	-	-	wild	Robinson et al. (1987)
<i>Cacajao melanocephalus</i>	40–50 (males)	13–21 (males)	3.0–4.5 (males)	Mittermeier et al. (2013)	-	-	190	-	1	wild	Mittermeier et al. (2013)
	30–40 (females)	13–21 (females)	2.4–3.0 (females)								

Campbell, 2007). Some groups are limited, with approximately 20 animals; however, groups with up to 200 individuals of both sexes have been reported (Bowler & Bodmer, 2009; Bowler, 2007).

Uakari monkeys are found in some countries of South America (Brazil, Colombia, Peru, and Venezuela, Figure 1b) and inhabit relatively restricted regions of the Amazon basin (Barnett et al., 2013; Boubli et al., 2008). In the genus *Cacajao*, the species with the largest geographic distribution is *C. melanocephalus* (golden-backed black uakari), which is found in forest regions north of the Brazilian Amazon and South of the Venezuelan Amazon (Boubli et al., 2021a). In contrast, other species of this genus have a more restricted geographical distribution. *C. homosi* (black-headed uakari) is limited to Brazil and Venezuela and is native to forests located to the south and west by the Rio Negro and to the east by the Rio Marauíá (Mittermeier et al., 2021). The species *C. ayresi* (Ayres black uakari) is found discontinuously along the Aracá River basin and is present only in Brazil (Amazonas State) and Venezuela (Boubli et al., 2021b). Finally, *C. calvus* (bald-headed uakari) is found in the Brazilian states of Amazonas and Acre and in the departments of Loreto and Ucayali in Peru (Aquino et al., 2022).

4.2 | Female reproductive morphophysiology

The ovaries of *C. calvus* are creamy-white with an ovoid shape and smooth surface, as the large antral follicles and CL do not protrude above the surface (Figure 5a). Females have an average ovarian

volume of 3.6 cm³ with no differences between the left and right ovary or according to different phases of the estrous cycle. The germinal epithelium is in cortical region of the ovary and contains follicles, including atretic follicles, at different developmental stages. In *C. calvus*, the largest pre-ovulatory follicle had a diameter of 8 mm (Mayor et al., 2013a).

The CL has a lobulated appearance and is delimited by condensed stromal tissue. The average diameter of the CL is 0.85 cm, and the largest CL almost completely occupied the stroma of the ovary. No differences in the CL characteristics between pregnant and nonpregnant females have been observed, but females in the advanced stages of pregnancy show a gradual regression that ends with the disappearance of the CL. Accessory CL have also been found in the species with a mean diameter of 0.2 cm (Mayor et al., 2013a).

The uterine tube of uakaries is simple, with an average length of 3.5 cm and without the formation of an ovarian bursa by the mesosalpinx (Mayor & López-Plana, 2021; Mayor et al., 2013a). As in *L. l. poeppigii*, the infundibulum has branched longitudinal folds with primary, secondary, and tertiary layers; however, only primary folds are observed in the isthmus. In addition, the lumen in the infundibulum is wider than that in other regions because the muscular layer of this region is thinner than that of the ampulla and isthmus regions.

The uterus is an elongated organ without uterine horns and has a single compartment called simplex uterus (Mayor & López-Plana, 2021; Mayor et al., 2013a). The fundus is globular, and the

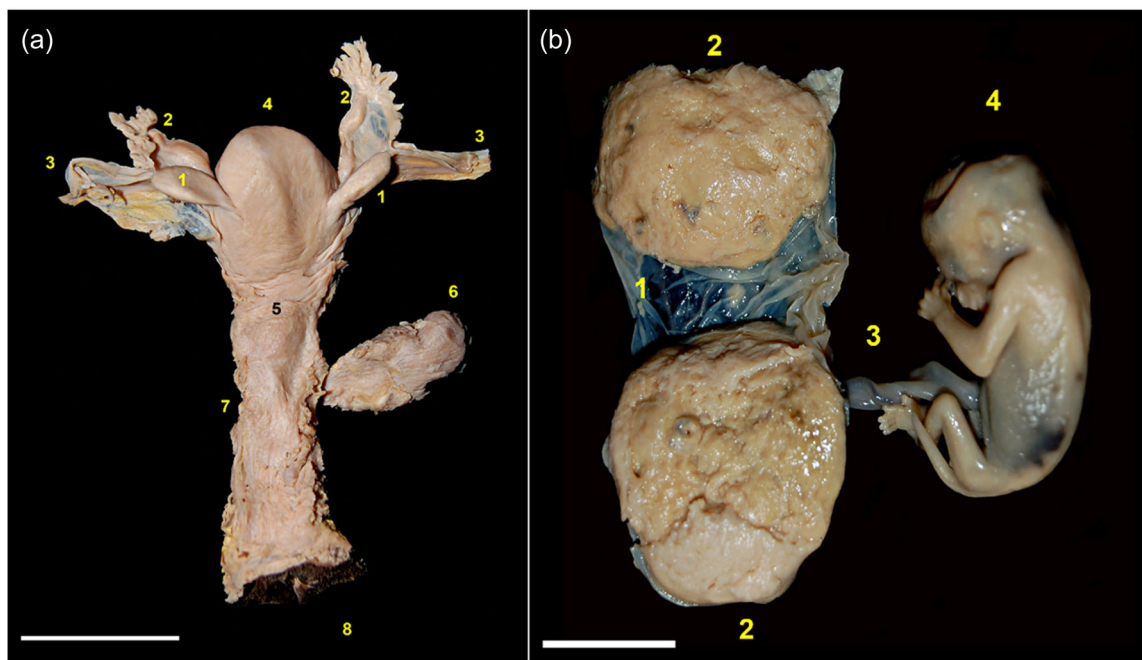


FIGURE 5 Female genital organs of the red uakari (*Cacajao calvus*). (a) Dorsal view of the genital organs in early follicular cycle: 1. Ovaries; 2. Uterine tubes; 3. Broad ligament of uterus; 4. Uterine body; 5. Cervix; 6. Urinary bladder; 7. Vagina; 8. Vulva. (bar: 2 cm). (b) Fetal membranes and fetus. The placenta is discoidal, deciduous, and hemochorial. This species has two discoid zones: 1. Chorioallantoic membrane; 2. Maternal-fetal contact discoid zone; 3. Umbilical cord; 4. Fetus. (bar: 2 cm). Source: adapted from Mayor and López-Plana (2021).

long cervix connects the uterine body to the vagina (Figure 5a). Macroscopically, the length of the uterine body in nonpregnant females is on average 1.67 cm, and is located completely in the pelvic cavity. In contrast, the uterine body in pregnant females enlarges up to 6.8 cm and extends into the abdominal cavity (Mayor et al., 2013a).

Changes in the uterine endometrium are observed throughout the estrous cycle. Nonpregnant females in the proliferative phase showed a gradual increase in the number of endometrial glands, which was directly related to the growth of antral follicles, preparing the endometrium for embryo implantation. At the end of the proliferative phase, the endometrium reaches a maximum thickness and high gland density. Glandular secretory activity, the secretory phase, begins with ovulation and is paralleled by endometrium thickening (Mayor et al., 2013a). Fibrin clots were observed during the early follicular growth (Mayor et al., 2019), suggesting endometrial hemostasis after desquamation of the functional layer and regulation bleeding in the menstrual cycle (Aedo et al., 2013).

In Neotropical primates, external signs of menstrual flow have been described in the genera *Alouatta*, *Ateles*, and *Sapajus* (Kaiser, 1947; Martin, 2012). Reports have demonstrated the occurrence of endometrial desquamation and slight bleeding at the end of the luteal phase in *Sapajus apella*, *Sapajus macrocephalus* and *Sapajus robustus* (Pissinatti et al., 2019). In *S. apella*, menstruation occurs through the constriction of straight, not spiral, endometrial arterioles (Carosi et al., 2005). Discrete menstruation has been observed in microscopic studies of smaller species (*Cebus* sp., *Sapajus* sp. and *Aotus* sp.; Mayor et al., 2019). Thus, the limited evidence of menstruation in primates may be related to the absence of spiral arteries in the endometrium, which is a common feature of many New World primate species (Aedo et al., 2013; Mayor et al., 2019).

The reproductive physiology in the Pitheciidae family remains poorly understood, with sparse information on reproductive cycles and endometrial characteristics (Barnett et al., 2013; Mayor et al., 2019). Uterine microscopy has been conducted on *C. calvus*; however, there is insufficient information to confirm menstrual activity in this species. Mayor et al. (2013a) reported the presence of

small amounts of collagen in the subepithelial region of the endometrium during the early follicular phase, suggesting nonvisible or absent menstrual bleeding. In another study, Mayor et al. (2019) evaluated the endometrium of *C. calvus* and did not observe hemosiderin clots suggesting no endometrial shedding (Figure 6).

The uterine cervix of nonpregnant and pregnant females has a constant length between 1.0 and 1.1 cm. The vaginal process of the cervix protrudes into the vagina, forming a 0.38 cm enfolding. The vagina has a mucosa with stratified squamous epithelium and various papillae in the lamina propria. The thickness of epithelium was greater in nonpregnant females in the follicular and luteal phases compared to pregnant and inactive females. Furthermore, nonpregnant females in the follicular phase had higher epithelial cornification than other females (Mayor et al., 2013a). Although no scientific study was found using vaginal cytology in *Cacajao* sp., these results suggest that vaginal cytology could be a successful methodology to characterize the estrous cycle in the uakari monkey.

After fertilization in the uterine tube, the embryo travels to the endometrium where implantation occurs. Throughout pregnancy, the endometrial glands progressively collapse, and the endometrium disappears due to the development of the due to the development of the placental discs and, thus, forming the maternal-fetal attachment (Mayor et al., 2013a). Pregnant females have a discoid-in-shape, hemochorial and deciduate placenta, with two discs as a region of maternal-fetal attachment (Figure 5b) (Mayor & López-Plana, 2021; Mayor et al., 2013a). No microscopic information was observed about the fetal membranes and the umbilical cord in the genus *Cacajao*.

4.3 | Reproductive biology

Limited information on the reproductive biology of *Cacajao* is available in the scientific literature. Despite reports of sequential mating of two males with the same female (Barnett et al., 2005; Barnett, 2005), it has been suggested that the genus *Cacajao* exhibits

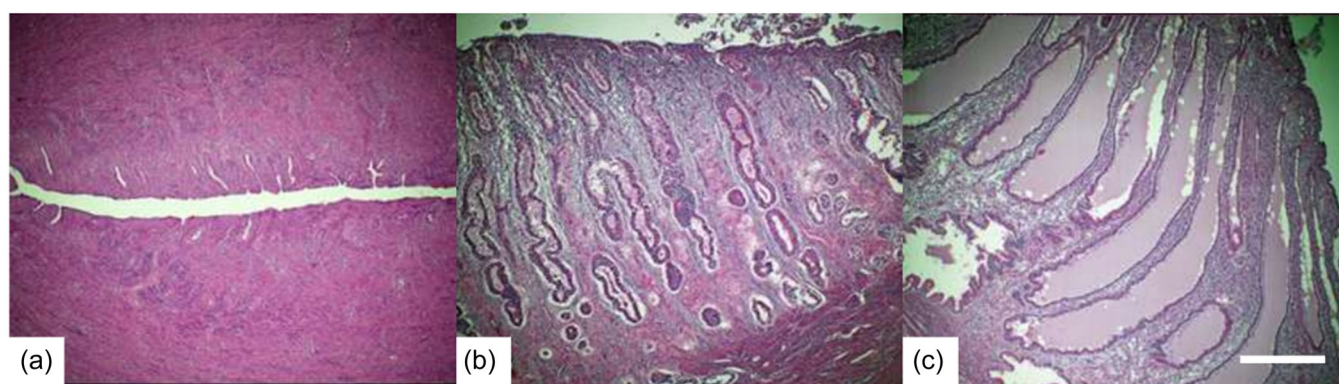


FIGURE 6 Photomicrographs of the uterine body of a nonpregnant female red uakari (*Cacajao calvus*) demonstrating the development of endometrial glands. (a) Early follicular-proliferative phase, (b) advanced follicular-proliferative phase, and (c) luteal-secretory phase of the reproductive cycle. H&E (bar: 0.5 mm). Source: adapted from Mayor and López-Plana (2021).

a monogamous mating system due to the absence of evident sexual dimorphism or social hierarchy with competition between males (Barnett, 2005; Fleagle, 2013; Lindenfors, 2002). During copulation of semi-captive uakaris, males smell the anogenital region of the female who rubs her genitals and presents herself in a quadrupedal mating position (Fontaine, 1981). The uakari is apparently a seasonal breeder, with the mating occurring from March to April, and parturitions in periods with greater food supply, between September and November in Central Amazon (Ayres, 1989) or December and March in Western Amazon (Aquino & Encarnación, 1994). Mayor and Bowler (2015) reported that there was a higher incidence of wild pregnant females of *C. calvus ucayalii* in the northeast region of the Peruvian Amazon between September and January. When receptive, females can mate several times with the same male (Bowler, 2007).

In the wild, female *C. calvus* reach sexual maturity at 3.5 years (Robinson et al., 1987). There is no detailed description of the estrous cycle, but the only scientific reference reports a large range in the duration of the estrous cycle from 14 to 48 days, an excessively long interval due to methodological limitations (Hayssen et al., 1993). Gestation lasts an average of 6 months, delivering at term only one newborn, which suckles for approximately 21 months (Ayres, 1989; Hayssen et al., 1993). *Cacajao melanocephalus*, *C. homosi*, and *C. ayresii* have not been successfully bred in captivity; therefore, descriptions of the estrous or menstrual cycle, duration of reproductive activity, and gestation are usually extrapolated from information about wild or semi-captive population of *C. calvus* (Barnett, 2005; Lindenfors, 2002).

Red uakaris exhibit a high degree of fission-fusion behavior with the formation of subgroups of one-male multifemale units (Bowler & Bodmer, 2009). Within this structure, dominant females may inhibit the reproduction of low-ranking females by providing less access to higher-quality food and by stimulating the release of higher levels of stress hormones. Another possibility is the prolonged period of parental care, which can place great demands on maternal energy metabolism and lead to longer birth intervals and reproductive inactivity (Mayor & Bowler, 2015). This behavior results in free-living populations having an especially high number of females with inactive ovaries compared to other primate species and a long birth interval of 25 months and 0.48 births/year/female, with the formation of one conceptus (Mayor & Bowler, 2015).

Physical characteristics and female reproductive parameters of woolly and uakari monkeys, such as sexual maturity, cycle and gestation duration, birth interval, number of offspring per gestation, and breeding condition are presented in Table 1.

5 | FINAL CONSIDERATIONS

The biological traits in the genera *Lagothrix* and *Cacajao* indicate that these endangered species are highly susceptible to population decline due to predatory hunting and habitat degradation. Their reproductive activity is slow, with the conception of a single

offspring, a long period of parental care, and delayed sexual maturation compared to small-sized Neotropical primates.

The uakari monkey is difficult to breed in captivity (Mayor & Bowler, 2015), and female woolly monkeys born in captivity experiencing complications during pregnancy and high infant mortality (Debyser, 1995). Breeding techniques that are routine in domesticated species are not easily adapted to wildlife. This could be due to species differences in reproductive morphophysiology, as well as mechanisms regulating the reproductive success. As a result, it becomes more challenging to apply reproductive biotechnologies, which are commonly used in domestic species and in the conservation of a few threatened species. (Pukazhenthil & Wildt, 2004). Assisted reproductive technologies (ARTs), include artificial insemination, embryo transfer, and in vitro fertilization. They are especially applied in nonhuman primates model species, like macaques and marmosets (Arakaki, 2023). However, to successfully use these technologies in females, it is important to have a good understanding of their reproductive morphophysiology. This knowledge is essential for determining the best place for depositing semen during artificial insemination and understanding their reproductive cycles, as protocols require the induction and synchronization of ovulation (Andrabi & Maxwell, 2007). Accurate information regarding the kinetics of embryonic development and maternal-fetal recognition in both genders is also fundamental for the development of embryo transfer.

However, to our knowledge, studies focusing on primate reproduction and application of biotechnology are limited to certain genera, such as *Callithrix*, *Aotus*, *Saimiri*, and *Sapajus* (de Lima Cardoso et al., 2021; Mayor et al., 2019; Monteiro et al., 2023; Tardif et al., 2012). Researchers are often hampered by a lack of basic biological data, and extrapolate from reproductive information generated in other taxa when applying ARTs. In Atelidae, the scarce available studies on the use of biotechnologies and hormonal analyzes were carried out in the genus *Alouatta* (Clarke & Glander, 1984; Kugelmeier et al., 2011) and in *Ateles geoffroyi* (Hernández-López et al., 2007), and no study was observed in Pitheciidae. However, although the ovarian cycle control has not been applied yet in Atelidae, researchers study in situ and ex situ populations using noninvasive reproductive endocrine monitoring techniques, providing information on female reproductive biology that will be essential for the application of ART (Arakaki, 2023).

There is currently a lack of basic information on the reproductive performance and morphophysiology in both families Atelidae and Pitheciidae, even inconclusive to classify the reproductive (estrous or menstrual) cycle. Researchers often struggle to habituate these animals in captivity and face significant difficulties in conducting reproductive studies in populations in the wild (Pinto et al., 2013). Monitoring free-living groups is only possible in populations with restricted home range by forest topography or forest fragments, which allows for easier group monitoring (Bowler & Bodmer, 2009) or by using samples of genital organs taking advantage of population deaths, both in captive conditions or in the wild (Mayor & Bowler, 2015). Thus, further studies focusing on endometrial tissue remodeling and the expression of collagen and uterine

metalloproteinases should be performed to identify the presence or absence of menstruation, act as a subsidy for studies related to the conservation of the genetic material of Amazonian species and correlate with the evolution and adaptation of this species.

AUTHOR CONTRIBUTIONS

Thyago Habner de Souza Pereira: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing—original draft (equal); Writing—review & editing (equal). **Pedro Mayor:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing—original draft (equal); Writing—review & editing (equal). **Janaina Serra Azul Monteiro Evangelista:** Conceptualization (equal); Methodology (equal); Project administration (equal); Writing—review & editing (equal). **Ana Kelen Felipe Lima:** Conceptualization (equal); Methodology (equal); Project administration (equal); Writing—review & editing (equal). **Rafael dos Santos de Andrade:** Methodology (equal); Writing—review & editing (equal). **Frederico Ozanan Barros Monteiro:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing—original draft (equal); Writing—review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The datasets during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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REFERENCES

Abbott, D. H. (1992). Reproduction in female marmoset monkeys, *Callithrix jacchus*. In W. C. Hamlett (Ed.), *Reproductive Biology of*

South American Vertebrates (pp. 245–261). Springer-Verlag. https://doi.org/10.1007/978-1-4612-2866-0_17

- Abondano, L. A., Ziegler, T. E., & Di Fiore, A. (2022). Reproductive endocrinology of wild female woolly monkeys (*Lagothrix lagotricha poeppigii*) during puberty, ovarian cyclicity, and pregnancy. *American Journal of Primatology*, 84(6), e23303. <https://doi.org/10.1002/ajp.23303>
- Aedo, S., Lira, P., Rivas, C., Narváez, P., & Campodónico, I. (2013). Ácido tranexámico en obstetricia y ginecología. *Revista de Obstetricia y Ginecología*, 8(3), 143–156.
- Andrabi, S. M. H., & Maxwell, W. M. C. (2007). A review on reproductive biotechnologies for conservation of endangered mammalian species. *Animal Reproduction Science*, 99(3–4), 223–243. <https://doi.org/10.1016/j.anireprosci.2006.07.002>
- De Andrade, R. S., Monteiro, F. O. B., El Bizri, H. R., Vicente, W. R. R., Guimarães, D. A. A., & Mayor, P. (2018). Fetal development of the Poeppig's woolly monkey (*Lagothrix poeppigii*). *Theriogenology*, 110, 34–43. <https://doi.org/10.1016/j.theriogenology.2017.12.022>
- Aquino, R., & Encarnación, F. (1994). Primates of Peru. *Primate Reproduction*, 40, 1–127.
- Aquino, R., de Queiroz, H. L., Paim, F. P., Boubli, J. P., Mittermeier, R. A., Ravetta, A. L., Shantee, S., Urbani, B., de Azevedo, R. B., Calouro, A. M., & Cornejo, F. M. (2022). *Cacajao calvus* (amended version of 2021 assessment). *The IUCN Red List of Threatened Species* 2022, e.T3416A210373615. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T3416A210373615.en>
- Arakaki, P. R. (2023). The Atelids. In A. R. Silva (Ed.), *Assisted Reproduction in Wild Mammals of South America* (pp. 140–154). CRC Press. <https://doi.org/10.1201/9781003231691>
- Ayres, J. M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution*, 18(7), 697–716. [https://doi.org/10.1016/0047-2484\(89\)90101-2](https://doi.org/10.1016/0047-2484(89)90101-2)
- Bakker, J., Louwerse, A. L., Remarque, E. J., & Langermans, J. A. M. (2018). Defining predictive factors for reproductive output in captive common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, 80(11), e22926. <https://doi.org/10.1002/ajp.22926>
- Barnett, A. A. (2005). *Cacajao melanocephalus*. *Mammalian Species*, 776, 1–6.
- Barnett, A. A., Bowler, M., Bezerra, B. M., & Defler, T. R. (2013). Ecology and behavior of uacaris (genus *Cacajao*). In L. Veiga, A. Barnett, S. Ferrari & M. Norconk (Eds.), *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris* (pp. 151–172). Cambridge University Press. <https://doi.org/10.1017/CBO9781139034210.020>
- Barnett, A. A., & Brandon-Jones, D. (1997). The ecology, biogeography and conservation of the uakaris, *Cacajao* (Pitheciinae). *Folia Primatologica*, 68(3–5), 223–235.
- Barnett, A. A., Castilho, C. V., Shapley, R. L., & Anicácio, A. (2005). Diet, habitat selection and natural history of *Cacajao melanocephalus* ouakary in Jaú National Park, Brazil. *International Journal of Primatology*, 26(4), 949–969.
- Blaffer, S., & Whitten, P. L. (1987). Patterning of sexual activity. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 370–384). University of Chicago Press.
- Boubli, J. P., Palacios, E., Urbani, B., Mittermeier, R. A., & Bezerra, B. M. (2021a). *Cacajao melanocephalus* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, e.T160875418A191697842. <https://doi.org/10.2305/IU-CN.UK.2021-1.RLTS.T160875418A191697842.en>
- Boubli, J. P., da Silva, M. N. F., Amado, M. V., Hrbek, T., Pontual, F. B., & Farias, I. P. (2008). A taxonomic reassessment of *Cacajao melanocephalus* Humboldt (1811), with the description of two new species. *International Journal of Primatology*, 29(3), 723–741. <https://doi.org/10.1007/s10764-008-9248-7>

- Boubli, J. P., Urbani, B., Mittermeier, R. A., & Bezerra, B. M. (2021b). *Cacajao ayresi* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021: e.T136419A191694077. <https://doi.org/10.2305/IUCN.UK.20211.RLTS.T136419A-191694077.en>
- Bowler, M. (2007). The ecology and conservation of the red uakari monkey on the Yavarí River, Peru. [Unpublished PhD thesis]. University of Kent, Canterbury.
- Bowler, M., Anderson, M., Montes, D., Pérez, P., & Mayor, P. (2014). Refining reproductive parameters for modelling sustainability and extinction in hunted primate populations in the Amazon. *PLoS One*, 9(4), e93625. <https://doi.org/10.1371/journal.pone.0093625>
- Bowler, M., & Bodmer, R. (2009). Social behavior in fission–fusion groups of red uakari monkeys (*Cacajao calvus ucayalii*). *American Journal of Primatology*, 71(12), 976–987. <https://doi.org/10.1002/ajp.20740>
- Carosi, M., Linn, G. S., & Visalberg, E. (2005). The sexual behavior and breeding system of tufted capuchin monkeys (*Cebus apella*). *Advances in the Study of Behavior*, 35, 105–149. [https://doi.org/10.1016/S0065-3454\(05\)35003-0](https://doi.org/10.1016/S0065-3454(05)35003-0)
- Castellanos, H., & Louis McCombs, H. (1968). The reproductive cycle of the new world monkey. *Fertility and Sterility*, 19(2), 213–227. [https://doi.org/10.1016/s0015-0282\(16\)36607-9](https://doi.org/10.1016/s0015-0282(16)36607-9)
- Castilla Torres, R. I., De Souza Jesus, A., Olazabal Loaiza, J., & Mayor, P. (2022). Dietas de primates no humanos del norte amazónico peruano. *Revista de Investigaciones Veterinarias del Perú*, 33(1), e22159. <https://doi.org/10.15381/rivep.v33i1.22159>
- Clarke, M. R., & Glander, K. E. (1984). Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In M. F. Small (Ed.) *Female primates: Studies by women primatologists*, (pp. 111–126). Alan R. Liss, Inc.
- Cornejo, F. M., Stevenson, P. R., Wallace, R. B., Ravetta, A. L., Valença-Montenegro, M. M., Rylands, A. B., & Messias, M. R. (2021). *Lagothrix lagotricha* ssp. *cana* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, e.T39962A192308612. <https://doi.org/10.2305/IUCN.UK.20211.RLTS.T39962A19-2>
- Critchley, H. O. D., Maybin, J. A., Armstrong, G. M., & Williams, A. R. W. (2020). Physiology of the endometrium and regulation of menstruation. *Physiological Reviews*, 100(3), 1149–1179. <https://doi.org/10.1152/physrev.00031.2019>
- Debyser, I. W. J. (1995). Platyrrhine juvenile mortality in captivity and in the wild. *International Journal of Primatology*, 16(6), 909–933. <https://doi.org/10.1007/bf02696110>
- Defler, T. R. (1989). Recorrido y uso del espacio en un grupo de *L. lagotricha* (Primates: Cebidae) mono lanudo o churucó en la Amazonia colombiana. *Trianea (Acta Científica y Tecnológica. Inderena)*, 3, 183–205.
- Ellis, K. M., Abondano, L. A., Montes-Rojas, A., Link, A., & Di Fiore, A. (2021). Reproductive seasonality in two sympatric primates (*Ateles belzebuth* and *Lagothrix lagotricha poeppigii*) from Amazonian Ecuador. *American Journal of Primatology*, 83(1), e23220. <https://doi.org/10.1002/ajp.23220>
- Estrada, A., Garber, P. A., Mittermeier, R. A., Wich, S., Gouveia, S., Dobrovolski, R., Nekaris, K. A. I., Nijman, V., Rylands, A. B., Maisels, F., Williamson, E. A., Bicca-Marques, J., Fuentes, A., Jerusalinsky, L., Johnson, S., Rodrigues de Melo, F., Oliveira, L., Schwitzer, C., Roos, C., ... Setiawan, A. (2018). Primates in peril: The significance of Brazil, Madagascar, Indonesia and the democratic republic of the Congo for global primate conservation. *PeerJ*, 6, e4869. <https://doi.org/10.7717/peerj.4869>
- Fernandez-Duque, E. (2012). Owl monkeys *Aotus* spp in the wild and in captivity. *International Zoo Yearbook*, 46(1), 80–94. <https://doi.org/10.1111/j.1748-1090.2011.00156.x>
- Di Fiore, A., & Campbell, C. J. (2007). The Atelines: Variations in ecology, behavior, and social organization. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder (Eds.), *Primates in Perspective* (pp. 155–185). Oxford University Press.
- Di Fiore, A., Chaves, P. B., Cornejo, F. M., Schmitt, C. A., Shanee, S., Cortés-Ortiz, L., Fagundes, V., Roos, C., & Pacheco, V. (2015). The rise and fall of a genus: Complete mtDNA genomes shed light on the phylogenetic position of yellow-tailed woolly monkeys, *Lagothrix flavicauda*, and on the evolutionary history of the family Atelidae (Primates: Platyrrhini). *Molecular Phylogenetics and Evolution*, 82, 495–510. <https://doi.org/10.1016/j.ympev.2014.03.028>
- Di Fiore, A., Link, A., & Campbell, C. J. (2011). The atelines: Behavioral and socioecological diversity in a New World radiation. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M. Strumpf (Eds.), *Primates in Perspective* (pp. 155–188). Oxford University Press.
- Di Fiore, A., Schmitt, C. A., & Fernandez-Duque, E. (2014). Morphometrics of wild woolly monkeys: Implications of sexual dimorphism in body and canine size. *American Journal of Physical Anthropology*, 153(S58), 106.
- Di Fiore, A., Spehar, S., Schmitt, C., & Link, A. (2009). Dispersal patterns in sympatric woolly and spider monkeys: Integrating molecular and observational data. *Behaviour*, 146(4–5), 437–470. <https://doi.org/10.1163/156853909x426345>
- Fleagle, J. (2013). *Primate Adaptation and Evolution* (3rd ed.). Academic Press.
- Fontaine, R. (1981). The uakaris, genus *Cacajao*. In A. F. Coimbra-Filho & R. A. Mittermeier (Eds.), *Ecology and Behavior of Neotropical Primates*. Academia Brasileira de Ciências.
- Fooden, J. (1963). A revision of the woolly monkeys (genus *Lagothrix*). *Journal of Mammalogy*, 44(2), 213–247.
- Ford, S. M., & Davis, L. C. (1992). Systematics and body size: Implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology*, 88(4), 415–468. <https://doi.org/10.1002/ajpa.1330880403>
- Groves, C. (2005). Order primates. In D. E. Wilson & D. M. Reeder (Eds.), *Mammal Species of the World* (pp. 111–184). The Johns Hopkins University Press.
- Hayssen, V., van Tienhoven, A., & van Tienhoven, A. (1993). *Asdell's Patterns of Mammalian Reproduction: A Compendium of Species-Specific Data*. Cornell University Press.
- Hernández-López, L., Cerda-Molina, A. L., Páez-Ponce, D. L., Rojas-Maya, S., & Mondragón-Ceballos, R. (2007). Artificial insemination in black-handed spider monkey (*Ateles geoffroyi*). *Theriogenology*, 67(2), 399–406. <https://doi.org/10.1016/j.theriogenology.2006.06.016>
- Hernández-López, L., Mayagoitia, L., Esquivel-Lacroix, C., Rojas-Maya, S., & Mondragón-Ceballos, R. (1998). The menstrual cycle of the spider monkey (*Ateles geoffroyi*). *American Journal of Primatology*, 44(3), 183–195. [https://doi.org/10.1002/\(sici\)1098-2345\(1998\)44:3](https://doi.org/10.1002/(sici)1098-2345(1998)44:3)
- Hershkovitz, P. (1987). The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): A preliminary report and critical review with the description of a new species and a new subspecies. *American Journal of Primatology*, 12(4), 387–468. <https://doi.org/10.1002/ajp.1350120402>
- Jesus, A. S., Castilla Torres, R. I., Quadros, J. C., Cruz, A. N., Valsecchi, J., El Bizri, H. R., & Mayor, P. (2022). Are larger primates less faunivorous? Consumption of arthropods by Amazonian primates does not fulfil the Jarman-Bell and Kay models. *Acta Amazonica*, 52(3), 208–217. <https://doi.org/10.1590/1809-4392202200842>
- Kaiser, I. H. (1947). Absence of coiled arterioles in the endometrium of menstruating New World monkeys. *The Anatomical Record*, 99(3), 353–367. <https://doi.org/10.1002/ar.1090990308>
- Kugelmeyer, T., del Rio do Valle, R., de Barros Vaz Guimarães, M. A., Pereira Carneiro Muniz, J. A., Barros Monteiro, F. O., & de Oliveira, C. A. (2011). Tracking the ovarian cycle in black-and-gold howlers (*Alouatta caraya*) by measuring fecal steroids and observing vaginal bleeding. *International Journal of Primatology*, 32(3), 605–615. <https://doi.org/10.1007/s10764-010-9490-7>
- Levi, T., & Peres, C. A. (2013). Dispersal vacuum in the seedling recruitment of a primate-dispersed Amazonian tree. *Biological*

- Conservation, 163, 99–106. <https://doi.org/10.1016/j.biocon.2013.03.016>
- Lima, M. C. M., Scalercio, S. R. R. A., Lopes, C. T. A., Martins, N. D., Oliveira, K. G., Caldas-Bussiere, M. C., Santos, R. R., & Domingues, S. F. S. (2019). Monitoring sexual steroids and cortisol at different stages of the ovarian cycle from two capuchin monkey species: Use of non- or less invasive methods than blood sampling. *Heliyon*, 5(7), e02166. <https://doi.org/10.1016/j.heliyon.2019.e02166>
- de Lima Cardoso, D., de Araújo Guimarães, D. A., Mayor, P., Ferreira, M. A. P., Tavares Dias, H. L., de Faria Espinheiro, R., & Barros Monteiro, F. O. (2021). Reproductive biology of owl (*Aotus* spp.) and capuchin (*Sapajus* spp.) monkeys. *Animal Reproduction Science*, 227, 106732. <https://doi.org/10.1016/j.anireprosci.2021.106732>
- Lindfors, P. (2002). Sexually antagonistic selection on primate size. *Journal of Evolutionary Biology*, 15(4), 595–607. <https://doi.org/10.1046/j.1420-9101.2002.00422.x>
- Lynset, O. (1968). Studies on reproduction in the goat: I. The normal genital organs of the non-pregnant goat. *Acta Veterinaria Scandinavica*, 9(3), 208–222. <https://doi.org/10.1186/BF03547868>
- Mack, D., & Kafka, H. (1978). Breeding and rearing of woolly monkeys. *International Zoo Yearbook*, 18(1), 117–122. <https://doi.org/10.1111/j.1748-1090.1978.tb00239.x>
- Martin, R. D. (2012). Reproductive characteristics of New World monkeys. *International Zoo Yearbook*, 46(1), 95–108. <https://doi.org/10.1111/j.1748-1090.2012.00165.x>
- Mayor, P., El Bizri, H., Bodmer, R. E., & Bowler, M. (2017). Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology*, 31(4), 912–923. <https://doi.org/10.1111/cobi.12870>
- Mayor, P., & Bowler, M. (2015). Low birthrates and high levels of female reproductive inactivity may characterize the reproductive biology of wild Peruvian red uakaris (*Cacajao calvus ucayalii*). *Journal of Medical Primatology*, 44, 27–34. <https://doi.org/10.1111/jmp.12155>
- Mayor, P., Bowler, M., & López-Plana, C. (2013a). Functional morphology of the female genital organs in the Peruvian red uakari monkey (*Cacajao calvus ucayalii*). *American Journal of Primatology*, 75(6), 545–554. <https://doi.org/10.1002/ajp.22132>
- Mayor, P., Bowler, M., & López-Plana, C. (2013b). Ovarian functionality in Poeppig's woolly monkey (*Lagothrix poeppigii*). *Animal Reproduction Science*, 136(4), 310–316. <https://doi.org/10.1016/j.anireprosci.2012.11.006>
- Mayor, P., Bowler, M., & LÓPEZ-PLANA, C. (2012). Anatomichistological characteristics of the tubular genital organs of the female woolly monkey (*Lagothrix poeppigii*). *American Journal of Primatology*, 74(11), 1006–1016. <https://doi.org/10.1002/ajp.22051>
- Mayor, P., & López-Plana, C. (2021). *Atlas de anatomia de espécies silvestres amazônicas. Volume III. Mamíferos, Órgãos Urinários e Órgãos Genitais*. Edufra.
- Mayor, P., Pereira, W., Nacher, V., Navarro, M., Monteiro, F. O. B., El Bizri, H. R., & Carretero, A. (2019). Menstrual cycle in four New World primates: Poeppig's woolly monkey (*Lagothrix poeppigii*), red uakari (*Cacajao calvus*), large-headed capuchin (*Sapajus macrocephalus*) and nocturnal monkey (*Aotus nancymae*). *Theriogenology*, 123, 11–21. <https://doi.org/10.1016/j.theriogenology.2018.09.019>
- Mittermeier, R. A., Boubli, J. P., Bezerra, B. M., & Urbani, B. (2021). *Cacajao hosomi* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, eT136640A191697668. <https://doi.org/10.2305/IUCN.UK.20211.RLTS.T13-6640A191697668.en>
- Mittermeier, R. A., Rylands, A. B., & Wilson, D. E. (2013). *Handbook of the mammals of the world, vol. 3. Primates* (1st ed.). Lynx Edicions.
- Monteiro, F. O. B. M., Silva, G. P., Pereira, T. H. S., Takeshita, R. S. C., Ruiz, J. C., & Mayor, P. (2023). The Aotidae. In A. R. Silva (Ed.), *Assisted Reproduction in Wild Mammals of South America* (pp. 126–139). CRC Press. <https://doi.org/10.1201/9781003231691>
- Mooney, J. C., & Lee, P. C. (1999). Reproductive parameters in captive woolly monkeys (*Lagothrix lagotricha*). *Zoo Biology*, 18(5), 421–427. [https://doi.org/10.1002/\(sici\)1098-2361\(1999\)18:5](https://doi.org/10.1002/(sici)1098-2361(1999)18:5)
- Nishimura, A. (2003). Reproductive parameters of wild female *Lagothrix lagotricha*. *International Journal of Primatology*, 24(4), 707–722. <https://doi.org/10.1023/A:1024681703616>
- Nowak, R. (1999). *Walker's Mammals of the World*. The John Hopkins University Press.
- Pereira, E. R., Pires, V. C. M. C., Fernandes, R. J., Pereira, D. K. S., Melo, F. R., Schell, R. K. W., Zarpelon-Schutz, A. C., & Pereira, K. F. (2020). Anatomia do sistema reprodutor feminino de *Alouatta belzebul* (Linnaeus, 1766). *Arquivo Brasileiro De Medicina Veterinária e Zootecnia*, 72(6), 2101–2110. <https://doi.org/10.1590/1678-4162-11859>
- Peres, C. A. (1994). Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in Central Amazonia: Comparisons with other atelines. *International Journal of Primatology*, 15(3), 333–372. <https://doi.org/10.1007/bf02696098>
- Pinto, L. P., Barnett, A. A., Bezerra, B. M., Boubli, J. P., Bowler, M., Cardoso, N. D. A., Caselli, C. B., Rodríguez, M. J. O., Santos, R. R., Setz, E. Z. F., & Veiga, L. M. (2013). Why we know so little: The challenges of fieldwork on the Pitheciids. In L. Veiga, A. Barnett, S. Ferrari & M. Norconk (Eds.), *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris* (pp. 145–150). Cambridge University Press. <https://doi.org/10.1017/CBO9781139034210.019>
- Pissinatti, T. A., Ribas, J. A. S., Maróstica, E., Pissinatti, A., & Ferreira, A. M. R. (2019). Ultrasound monitoring of the uterus and ovaries of dominant and subordinate females of yellow-breasted capuchin (*Sapajus xanthosternus*) and robust tufted capuchin (*Sapajus robustus*) in captive colonies during the ovarian cycle and anestrus periods. *Pesquisa Veterinária Brasileira*, 39(12), 989–996. <https://doi.org/10.1590/1678-5150-PVB-6174>
- Pukazhenthi, B. S., & Wildt, D. E. (2004). Which reproductive technologies are most relevant to studying, managing and conserving wildlife? *Reproduction, Fertility, and Development*, 16(2), 33. <https://doi.org/10.1071/rd03076>
- Ramirez, M. (1980). Grouping patterns of the woolly monkeys, *Lagothrix lagotricha*, at the Manu National Park, Peru. *American Journal of Physical Anthropology*, 52, 269.
- Reavey, J. J., Maybin, J. A., & Critchley, H. O. (2018). Physiology of menstruation. In R. A. Kadir, P. D. James & C. A. Lee (Eds.), *Inherited Bleeding Disorders in Women* (2nd ed.). Wiley-Blackwell.
- Robinson, J. G., & Redford, K. H. (1986). Intrinsic rate of natural increase in Neotropical Forest mammals: Relationship to phylogeny and diet. *Oecologia*, 68(4), 516–520. <https://doi.org/10.1007/bf00378765>
- Robinson, J. G., Wright, P. C., & Kinzey, W. G. (1987). Monogamous cebids and their relatives: Intergroup calls and spacing. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate Societies*. Chicago University Press.
- Ross, C. (1988). The intrinsic rate of natural increase and reproductive effort in primates. *Journal of Zoology*, 214(2), 199–219. <https://doi.org/10.1111/j.1469-7998.1988.tb04717.x>
- Ross, C. (1991). Life history patterns of new world monkeys. *International Journal of Primatology*, 12(5), 481–502. <https://doi.org/10.1007/bf02547635>
- Schmitt, C. A. (2010). Comparative behavior, development and life history of wild juvenile atelin primates (*Ateles belzebuth* and *Lagothrix poeppigii*). [Unpublished doctoral dissertation]. New York University, New York.
- Senger, P. L. (2005). *Pathways to pregnancy and parturition* (2nd ed.). Current Conceptions Inc.
- Shanee, S., Cornejo, F. M., Aquino, R., Mittermeier, R. A., & Vermeer, J. (2021a). *Lagothrix flavicauda* (amended version of 2019 assessment). *The IUCN*

- Red List Threatened Species* 2021, e.T39924A192307818. <https://doi.org/10.2305/IUCN-UK.2021-1.RLTS.T39924A192307818.en>
- Shanee, S., Stevenson, P. R., de la Torre, S., Moscoso, P., Ravetta, A. L., & Muniz, C. C. (2021b). *Lagothrix lagothricha* ssp. *poepigii* (amended version of 2020 assessment). *The IUCN Red List Threatened Species*. 2021, e.T39927A192308336. <https://doi.org/10.2305/IUCN-UK.2021-1.RLTS.T39927A192308336.en>
- Silvestre, T., Zanetti, E. S., Duarte, J. M. B., Barriento, F. G., Hirano, Z. M. B., Souza, J. C., & Passos, F. C. (2017). Ovarian cycle of southern brown howler monkey (*Alouatta guariba clamitans*) through fecal progesterone measurement. *Primates*, 58, 131–139. <https://doi.org/10.1007/s10329-016-0561-z>
- Slayden, O. D., & Calhoun, A. (2018). The primate uterus: Cyclic changes. *Encyclopedia of Reproduction*, 2, 312–319.
- Srivastava, P. K., Cavazos, F., & Lucas, F. V. (1970). Biology of reproduction in the squirrel monkey (*Saimiri sciureus*): I. The estrus cycle. *Primates*, 11(2), 125–134. <https://doi.org/10.1007/bf01731138>
- Stevenson, P. R. (2002). Frugivory and seed dispersal by woolly monkey (*Lagothrix lagothricha*) at Tinigua National Park, Colombia. [Unpublished doctoral dissertation]. State University of New York, New York.
- Stevenson, P. R., Defler, T. R., de la Torre, S., Moscoso, P., Palacios, E., Ravetta, A. L., Vermeer, J., Link, A., Urbani, B., Cornejo, F. M., Guzmán-Caro, D. C., Shanee, S., Mourthé, Í., Muniz, C. C., Wallace, R. B., & Rylands, A. B. (2021a). *Lagothrix lagothricha* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, e.T160881218A192309103. <https://doi.org/10.2305/IUCN-UK.2021-1.RLTS.T160881218A192309103.en>
- Stevenson, P. R., Link, A., & Guzmán-Caro, D. C. (2021b). *Lagothrix lagothricha* ssp. *lugens* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, e.T39926A192308084. <https://doi.org/10.2305/IUCN-UK.2021-1.RLTS.T39926A192308084.en>
- Stevenson, P. R., Quinones, M. J., & Ahumada, J. A. (1994). Ecological strategies of woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia. *American Journal of Primatology*, 32(2), 123–140. <https://doi.org/10.1002/ajp.1350320205>
- Sutherland, W. J., Atkinson, P. W., Broad, S., Brown, S., Clout, M., Dias, M. P., Dicks, L. V., Doran, H., Fleishman, E., Garratt, E. L., Gaston, K. J., Hughes, A. C., Le Roux, X., Lickorish, F. A., Maggs, L., Palardy, J. E., Peck, L. S., Pettorelli, N., Pretty, J., ... Thornton, A. (2021). A 2021 horizon scan of emerging global biological conservation issues. *Trends in Ecology & Evolution*, 36(1), 87–97. <https://doi.org/10.1016/j.tree.2020.10.014>
- Tardif, S., Carville, A., Elmore, D., Williams, L. E., & Rice, K. (2012). Reproduction and breeding of nonhuman primates. In C. R. Abbe, S. Tardif, K. Mansfield & T. Morris (Eds.), *Nonhuman primates in biomedical research* (pp. 197–249). Academic Press. <https://doi.org/10.1016/B978-0-12-381365-7.00008-X>
- Timmer, S. (2006). The influence of nutrition on the health status of captive woolly monkeys. [Unpublished masters thesis]. Wageningen University, The Netherlands.
- Vermeer, J., Wallace, R., & Shanee, S. (2021). *Lagothrix lagothricha* ssp. *tschudii* (amended version of 2020 assessment). *The IUCN Red List Threatened Species* 2021, e.T39963A192308920. <https://doi.org/10.2305/IUCN-UK.2021-1.RLTS.T3-9963A192308920.en>
- Wildman, D. E., Chen, C., Erez, O., Grossman, L. L., Goodman, M., & Romero, R. (2006). Evolution of the mammalian placenta revealed by phylogenetic analysis. *Proceedings of the National Academy of Sciences USA*, 103(9), 3203–3208.
- Williams, L. (1967). Breeding Humboldt's woolly monkey *Lagothrix lagothricha* at Murrayton Woolly Monkey Sanctuary. *International Zoo Yearbook*, 7, 86–88. <https://doi.org/10.1111/j.1748-1090.1967.tb00329.x>
- Young, A. (1972). The primate umbilical cord with special reference to the transverse communicating artery. *Journal of Human Evolution*, 1(4), 345–359. [https://doi.org/10.1016/0047-2484\(72\)90111-x](https://doi.org/10.1016/0047-2484(72)90111-x)

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