




RESEARCH ARTICLE

Clitoral length in immature and mature captive tufted capuchin (*Sapajus* spp.) females: A cross-sectional study

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Abstract

Quantitative data on female external genital morphology are sporadic in the primate literature, and the intraspecific and interfemale variation is especially under investigated (e.g., external clitoris length). Since in most anthropoid primate species female external genitals are relatively small and often hidden, for those species whose external clitoris is described as hypertrophic, external genital resemblance may represent a source of confusion in distinguishing the sexes at a distance. This is the case of both captive and wild tufted capuchin (*Sapajus* spp.) infants. We provided data on external clitoral length and investigated differences in this trait at different ages in a captive female tufted capuchin population. Since likely allometric growth describes changes in relative dimensions of parts of the body that are correlated with changes in overall size, clitoris length has been analyzed by using body weight as a covariate. We measured clitoral length by adapting a technique developed for spotted hyenas (*Crocuta crocuta*). Our results suggest that the small body size may be only in part responsible of the perception of long clitoris in female infants, since the clitoris is actually longer in immature females compared to adult ones and its size is inversely related to body weight. While the cross-sectional nature of these data does not allow for conclusive interpretation of the results, we tentatively suggest this phenomenon as a transient male-mimicry by immature females. Our study contributed to the description of normative data in a clitoral trait, thus providing foundation for future studies about causal mechanisms and possible adaptive function(s).

KEYWORDS

external clitoris, immature sexual mimicry, negative allometry

1 | INTRODUCTION

First described in early papers (e.g., Gerhardt, 1909; Pehrson, 1914), much of our understanding of nonhuman primate female external genital appearance has stemmed from research conducted primarily in the first half of 20th century. Early papers qualitatively characterized external genital variability in shape, size, length, and color in various primate species and provided detailed descriptions and illustrations, mostly emphasizing intersexual and interspecific differences (e.g.,

Harms, 1956; Hershkovitz, 1977; Hill, 1933, 1953, 1958, 1960, 1962; Pocock, 1918, 1920, 1925). Quantitative data on female external genital morphology, however, are sporadic, and the intraspecific and interfemale variation is particularly under investigated (e.g., external clitoris size, but see qualitative observations in *Ateles*, Campbell & Gibson, 2008). The only quantitative data we are aware of are those by Drea and Weil (2008) who obtained a set of external genital measurements (external clitoris length, width, diameter and circumference; meatus length and distance; anogenital distance) in

captive adult *Lemur catta*, and Goldschmidt and colleagues (2009) who measured external clitoris length in captive *Macaca mulatta* at different age classes.

The external clitoris of tufted capuchins (*Sapajus* spp.) consists of a shaft that is ventrally grooved to the tip with the urethral opening at its base (Hill, 1960). The apex of the shaft slightly expands into a *glans clitoridis*, which is normally flattened and button-like shaped. When relaxed, the clitoris is enveloped in a preputial fold, which originates from the *labia minora*. However, when fully erect the clitoris becomes more visible. The base of the clitoris and the skin surrounding the vagina consist of darkly pigmented sparsely haired papillated tissue which corresponds to the development of the labioscrotal swelling into *labia majora* (Hill, 1960; Lima et al., 2015; Wislocki, 1936). Scientific literature describes the clitoris of tufted capuchins as resembling male penis (*Cebus* spp.: "...it is more penis-like" in Pocock, 1920; "The clitoris is shaped very much like the penis..." in Hill, 1960; *C. apella*: "...resembles the penis of male individuals" in Lima et al., 2015; "...the clitoris is developed like the penis" in Teixeira et al., 2015). In fact, external genital resemblance may, in some species and at different ages, represent a source of confusion in distinguishing the sexes at a distance (e.g., strepsirrhines, Ankel-Simons, 1983; juvenile *Alouatta palliata*, Clarke, 1990; Clarke, Zucker, Ford, & Harrison, 2007, Wislocki, 1936). This is what has been described in wild and captive tufted capuchins, whose infants have often been inaccurately sexed by human observers (Fragaszy, Visalberghi, & Fedigan, 2004; Hill, 1960; personal observation). In this species, however, inaccurate sexing is apparently limited to infancy, prompting us to question if the greater visibility of the clitoris in immature individuals (which is the cause for the reported confusion) might simply be due to different body proportions at different ages.

The insight that changes in proportion, as related to the growth of body size, are a major factor in evolution, has been especially significant for the studies on the relative growth of organs (Klingenberg, 1996). The growth of body parts at different rates, and the resulting variations in body proportions (i.e., allometry), can be considered with respect to either evolution (i.e., comparing adult individuals of related species) or development (i.e., comparing individuals of the same species and different age and size; Bertalanffy & Pirozynski, 1952, Gould, 1966, Huxley, 1932). Three main types of allometry have been distinguished, such as static (size allometry, i.e.,

variation among same age individuals belonging to the same population), evolutionary (covariation of changes in different traits along phylogenetic branches), and ontogenetic allometry (Cock, 1966). The latter (growth allometry; Huxley & Tessier, 1936), potentially interesting for the present study, deals with covariation among characters during growth. In this case, when longitudinal data on the same individuals along developmental stages cannot be obtained, data on different specimens at different ages (i.e., cross-sectional data) are used (Cock, 1966; Klingenberg, 1996). In fact, cross-sectional data are routinely used for estimating a population's ontogenetic trajectory or average growth pattern (see Leigh, 2006; Mitteroecker, Gunz, Windhager, & Schaffer, 2013; Smith, Crummet, & Brandt, 1994).

Considering the lack of normative data regarding external clitoris size in tufted capuchins, and based on the difficulty in sexing infants at a distance (see Figure 1), this study first aims to establish normal standards for the external clitoris length, by using standardized measurements in a sample of captive tufted capuchins (*Sapajus* spp.) at different ages. Second, by using cross-sectional data, we aim to determine if a negative (ontogenetic) allometry between body size and clitoris length can provide an explanation for the clitoris being less visible at later stages in life.

2 | METHODS

2.1 | Animal subjects

The tufted capuchin females contributing to this study ($N = 24$ ranging in age from 2 days to 38 years) were all housed at the National Institutes of Health (Animal Center, NICHD, Poolesville, MD; Table 1). Animals were members of different social groups living in different housing conditions according to their group size (a large social group, $N = 26$ individuals housed in an outdoor corncrib from May to October and in indoor runs from November to April; two smaller social groups, $N = 6$ individuals, housed either in indoor runs from May to October and indoor cages from November to April, or in indoor cages year round). All animals were fed Purina New World Monkey chow twice a day, various types of fruits and nuts once a day, and had continuous access to water. Different subsets of the animal sample were used for the clitoral study.

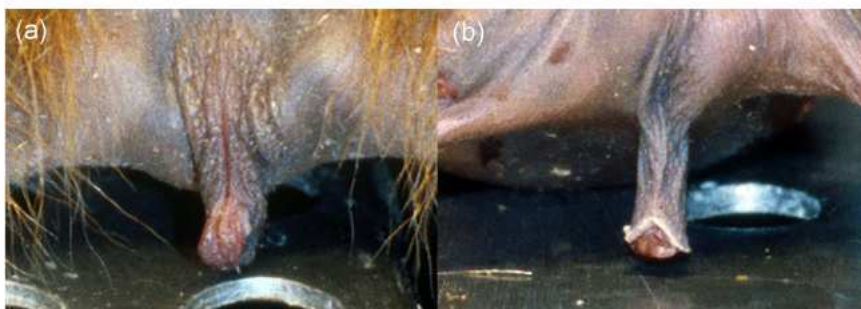


FIGURE 1 External genitals in newborn twins: (a) female and (b) male

TABLE 1 Female individuals, age at measurement and number of clitoral length measurements

Clitoris			
Females	Age at measurement yrs. or mos.		No. of measurements
	First	Last	
Lychee	4 mos	1.75	4
Mara	5 mos	11 mos	2
Liv	6 mos	1.83	4
Sam	9 mos	2.08	4
Ivory	1.08	2.5	4
Lyla	2.33	3.97	4
Sagan	2.92	4.25	4
Claire	3.17	4.5	4
Spider	3.25	4.25	3
Shannon	4.5	5.47	3
Cathead	5.25	5.66	4
Magic	5.58	6.97	4
Lorena	5.58	6.97	4
Mocha	6.83	8.25	4
Lee	8.25	9.58	4
Lucy ^a	13.0	15.0	(1)
Suki	13.58	14.97	4
Jasmine	15.0	16.0	5
Shinade ^a	15.2	16.6	(1)
Carlina	16.83	18.08	5
Isabella	18.0	20.0	5
Coco	36.0	38.0	3
Total			80

Abbreviations: mos, months; yrs, years.

^aTwo females whose clitoral measurements could not be performed due to the extreme short clitoris, however, contributing to analyses with a length set by default at 1 mm.

2.1.1 | Clitoral length measurements

During routine semiannual TB testing at the Animal Center (NICHD, Poolesville, MD), animals ($N = 22$, aged 4 months to 38 years, tested between December 1999 and May 2001) were immobilized via intramuscular injections of a combination of hydrochloride ketamine and acepromazine 10–15 mg/kg depending on body weight). Following immobilization, we recorded body weight and clitoral length for each subject (see below). Each anesthetized monkey was placed in supine position, with the animal's legs spread apart. Clitoral length was measured via a modified version of a technique developed for clitoral measurements in spotted hyenas (*Crocuta crocuta*) by Drea et al. (1998). A metal washer (4 cm in diameter, with an internal hole of 1 cm in diameter) was placed over the clitoris and the clitoris

pulled through the hole in the washer. A “noose,” made of a loop of dental floss with a weight attached to one end, was tied under the *glans clitoridis* after a gentle extrusion from the prepuce and pulled taught. The washer was stabilized against the pubic bone, providing a standardized reference point for measurement. The floss was then hung over a PVC pipe (at about 50 cm from the animal's body) with the weight dangling freely, thereby pulling the clitoris with a standardized tension corresponding to the weight. After experimenting with various weights, we found that 36 g provided the least amount of tension necessary to fully extend the clitoris for accurate measurement. The extended clitoris was then measured (from base to end of glans) by placing a ruler at a right angle on the washer and holding the floss parallel to the ruler (Figure 2a–c). Two measurements were obtained for each subject by two observers (M. C. and A. U.) and averages were later used for analyses. Each female subject was measured during a minimum of 2 to a maximum of 6 TB testing therefore, contributing differently to the data set. For two adult females, whose clitoris was too short to fit the washer and could not be measured, clitoris length was set to a default of 1 mm (Table 1 and Figure 2d). Although clitoral measurements were obtained with standardized method and weight for all subjects, an uneven response to a given tension by different sized clitorises and/or different tissue elasticity at different ages might be expected however, it was unquantifiable. Additionally, due to the tension applied, clitoral length data can neither reflect *Sapajus* actual clitoris length nor be used for interspecific comparisons, but exclusively for comparisons in this study at the interindividual level.

2.2 | Ethical note

Protocol and procedures employed in this study were ethically reviewed and approved and the study was conducted in accordance with the NIH Guide for the Care and Use of Laboratory Animals (approved Animal Study Proposal ASP 9#98 024). We also adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

2.3 | Statistical analysis

We divided our sample in three age classes (infants [I], 0–1 year old; juveniles [JUV], 1.1–4 years old; adults [A], 4.1–38 years old). Transition from infancy to juvenile stage was set at 1 year (age at weaning; Fragaszy & Adams-Curtis, 1998) whereas transition to maturity was set at the age of first conception (4 years) based on youngest age at first delivery reported in this species (about 4.5 years) and duration of gestation (160 days; Fragaszy & Adams-Curtis, 1998). To verify the transition between the juvenile and the mature phase in our animal sample, female body weight data were plotted against age (x-axis). We investigated the relationships between clitoral length at age groups first by analysis of variance (ANOVA; as done by Goldschmidt et al., 2009 and Hawkins, Dallas, Fowler, Woodroffe, & Racey, 2002)

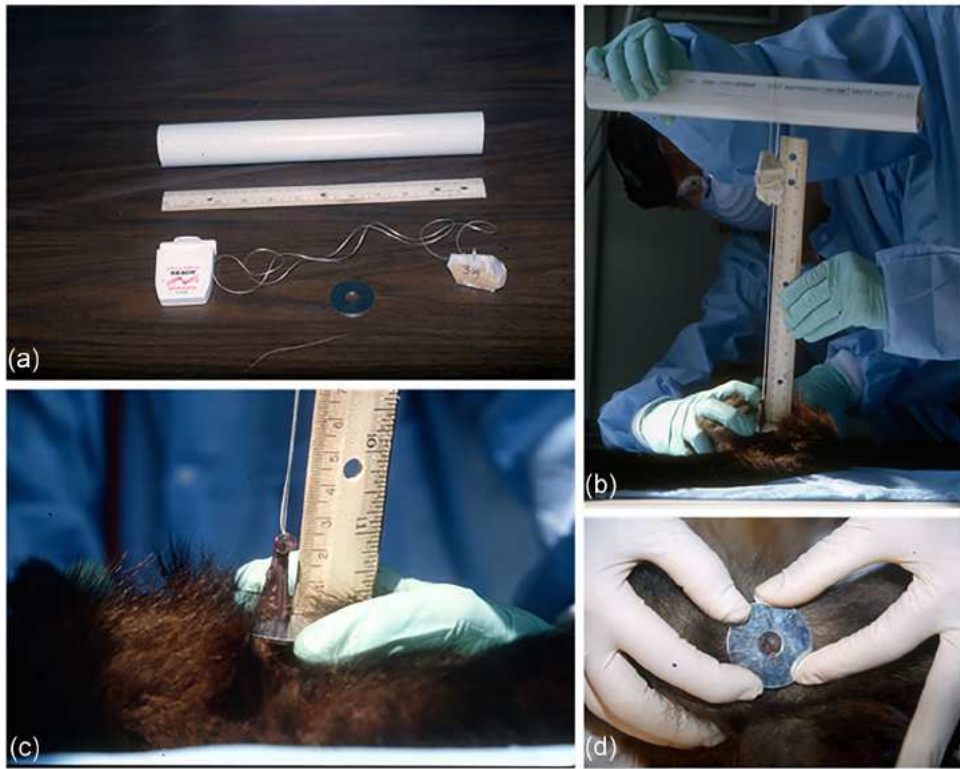


FIGURE 2 Method used for clitoral measurements (modified from technique developed by Drea et al. (1998) to measure clitoral length in spotted hyenas, *Crocuta crocuta*). (a) materials used (PVC pipe, dental floss, 36 g stone; washer); (b) clitoral measurements (see text for details); (c) close up of clitoral measurement (female Magic, 5-year old); (d) adult female with an extremely short clitoris which could not be measured by using this technique (female Lucy, DOB not known, not less than 13-year old)

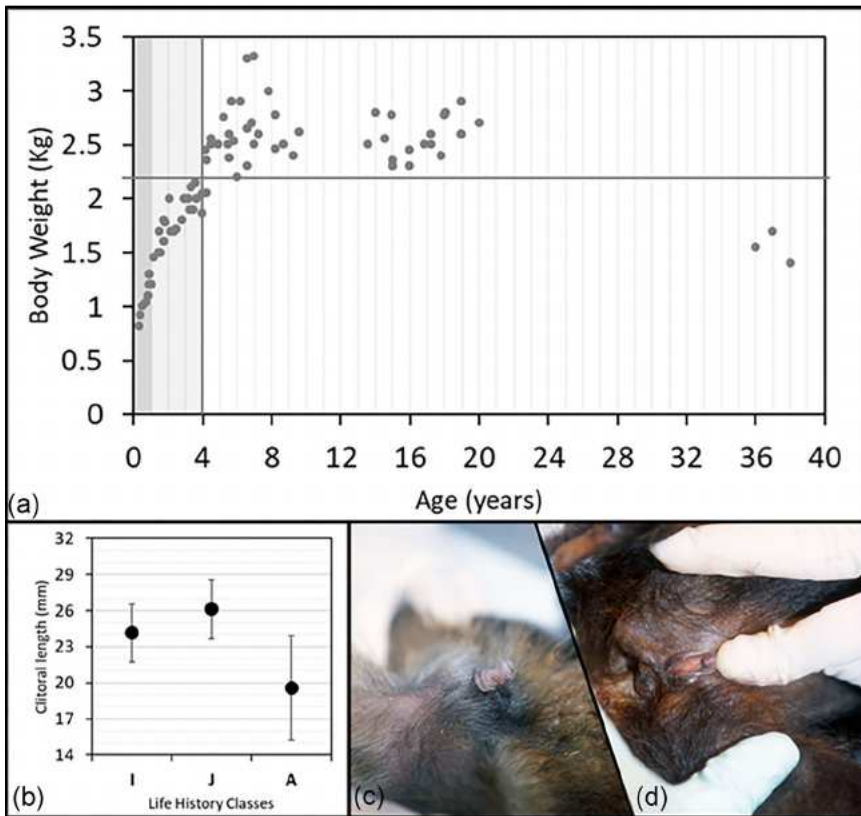


FIGURE 3 (a) Plot of body weight vs. age of 22 tufted capuchin (*Sapajus* spp.) females. Dark grey band stands for infants, I (0–1 year); light grey band stands for juveniles, J (1.1–4 years); white band stands for adults, A (4.1–38 years). Vertical grey line identifies the transition between immature and mature phase. (b) Clitoral mean length (SD bars) for each life history class. (c) Clitoris appearance in a representative infant female (6-mo. old). (d) Clitoris appearance in a representative old-adult female (37-years old). A, adult; I, infant; J, juvenile

and second by analysis of covariance (ANCOVA), using body weight as a covariate. For significant ANOVA outputs, we performed planned contrast analyses. Finally, to analyze the variability of clitoral length at different body weights and ages, data were log-transformed and a regression analysis was carried out.

3 | RESULTS

We plotted body weight versus age and set the age at maturity to 4 years (Figure 3a, vertical line). We observed age related differences in body weight that suggested a continuous and rapid increase from birth to maturity, a plateau during early and mid-adulthood (body weight never below 2.2 kg; Figure 3a, horizontal line), followed by a decrease in body weight in senescence (congruent pattern with longitudinal body weight and skeletal data, Fragaszy & Adams-Curtis, 1998; Jungers & Fleagle, 1980). In our sample clitoral length ranged from 1 to 30 mm (Table 2). All female infants observed in the colony (as well as some not included in the sample measured) showed, without exception, a prominently long clitoris ($N = 6$). Clitoris length differed among three age classes, $F(2, 78) = 21.7$, $p = .001$ (Figure 3b), with adult females having the smallest size, as shown in Figure 3 by comparing infant's (Figure 3c) and adult's (Figure 3d) clitoris, contrast analyses: A vs. IM, $F(1, 75) = 61.5$, $p = .001$; A vs. J, $F(1, 72) = 37.4$, $p = .001$; A vs. I, $F(1, 57) = 7.2$, $p = .009$. When the body weight was taken into account (ANCOVA) clitoris length differed among three age classes as well, $F(2, 77) = 11.2$, $p = .001$. Regression revealed clitoral length as inversely correlated to both age ($R = -0.6$, $p < .001$) and body weight ($R = -0.37$, $p < .001$; Figure 4).

4 | DISCUSSION

Allometry designates the changes in relative dimensions of parts of the body that are correlated with changes in overall size. Specifically, ontogenetic allometry shows these changes in the context of growth. Results presented in this study are a first step in characterizing the clitoris in tufted capuchins by providing data on one of its traits (i.e., length) and investigating differences in this trait at different ages (from infant to adult individuals). Our data support the qualitative

perception that immature female capuchins have longer clitorises than mature females. In fact, our results confirm that not only the naturally body growth may be in part responsible of a biased human perception, but that the clitoris is actually longer in immature females compared to adult ones.

In tufted capuchin immature individuals, the prominent clitoris represents a source of confusion in sex determination (in addition to a sessile scrotum in immature males; Fragaszy et al., 2004; Napier & Napier, 1967). However, our species is not the only challenging case of visually equivocal external genitalia in immature animals. Both Wislocki (1936) and Hill (1962) reported difficulties in sexing immature individuals in mantled howlers (*A. palliata*). Clarke et al. (2007) stated that observational studies of free-ranging juvenile mantled howlers are impeded by visually undifferentiated genitalia. In contrast, the hypertrophic and pendulous clitoris in *Ateles*, instead of confusing sexual determination, is used as key for sexing both newborn and monomorphic adult individuals (Campbell & Gibson, 2008).

In the diverse landscape of size and morphology of primate species clitorises, *Sapajus* and *Cebus* are listed together with *Ateles*, *Brahyteles* and *Lagothrix* as the five platyrrhine genera characterized by clitoral hypertrophy (Dixon, 2012). As stated by Campbell (2017), the hypertrophy concept is usually applied when size goes beyond normal proportions, yet "normal proportions" of clitorises in the various primate species may greatly vary. Normative data regarding clitoral size are scanty in the primate literature. Goldschmidt et al. (2009) measured the clitoral lengths of a large sample of captive *M. mulatta* females ($N = 285$) and, as in tufted capuchins, found significant variability in clitoral length at different age classes (infant, juvenile, young adult, and adult). However, they found an opposite trend if compared to our study species, with a positive correlation between clitoral length and age (also known in human females, see in Goldschmidt et al., 2009). Similarly, Drea and Weil (2008) reported quantitative data of female *L. catta* external genital morphology (e.g., anogenital distance, external clitoris length/diameter/circumference/width, meatus length/distance) and revealed a plateau in clitoral length at puberty. Differently, in *Ateles* genus, the distinctive and well known clitoral conspicuity has been reported as starting from birth and lasting throughout life (Hill, 1960). Nevertheless, interfemale variability in both clitoral length (*Ateles* spp.) and color (*A. belzebuth belzebuth* and *A. b. chamek*) has been reported as a useful trait for individual female and group membership identification (Campbell & Gibson, 2008). Unfortunately, no systematic

TABLE 2 Clitoral length (mm) in a colony of *Sapajus* spp.

Age group (age range, yrs)	No. Females	No. Measurements	Average length	Standard deviation	Min	Max
Infant (0–1)	4	7	24.1	2.39	20	26
Juvenile (1.1–4)	5	22	26.1	2.45	21	30 ^a
Adult (>4.1)	13	51	18.8	5.60	1 ^b	29
Total	22	80				

^aMaximum length by a young juvenile (Liv; 1.5 yrs old).

^bMinimum length by two adult subjects (Shinade and Lucy; from 13 to 16 yrs old).

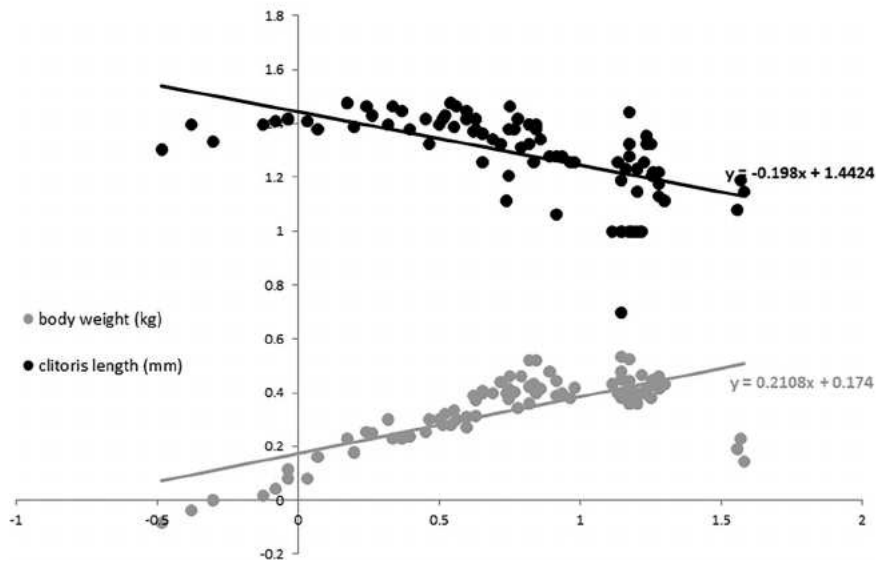


FIGURE 4 Scatter plot of body weight and clitoris length vs. age (all data were Log-transformed). Trend lines and associated equation are shown for each data set

data on clitoral length are available for these species. A genetic component to explain intraspecific variation in clitoral length has been hypothesized in both *Ateles* (differences between matriline; Campbell & Gibson, 2008) and *M. mulatta* (inheritance effects for clitoris presence/absence; Goldschmidt et al., 2009).

Clarification of potential clitoral functions in nonhuman primates is needed (Dixon, 2012), and functional hypotheses explaining interspecific variation on clitoral appearance are limited to those species demonstrating potentially related behavioral patterns or traits. In *Ateles*, for example, the possible role of clitoris in chemical communication of the female's reproductive state, is emphasized (Klein, 1971). In addition, observations of diverse clitoris-directed behaviors (Campbell, 2004; Pastor-Nieto, 2000) prompted researchers to hypothesize an array of functions for the extremely enlarged clitoris (the scent-marking and chemical signaling function, Klein, 1971, Pastor-Nieto, 2000; the sex distant identification function in a monomorphic species, Eisenberg & Kuehn, 1966; the "guide" facilitating male penetration function, Campbell, 2006; identification of adult females from a distance, Campbell & Gibson, 2008), all of which potentially correlate with clitoral peculiarities.

Since in most anthropoid primate species female external genitalia are relatively small and often hidden (Ankel-Simons, 2010; Dixon, 2012), the prominently long external clitoris observed in immature capuchins might tentatively be interpreted as a form of male mimicry (male-like appearance of female external genitalia, Fragaszy et al., 2004; Hill, 1960) and not related to the sexual-reproductive context. Virtually indistinguishable infants and juveniles have been described in howler monkeys as well. In this species, however, resemblance between sexes is based on a sort of undifferentiated morph which entails both external genitalia and behavior (Clarke, 1990; Clarke et al., 2007). Juvenile monomorphism in this species has been hypothesized as related to the advantage juveniles would take in looking immature and nonthreatening thus delaying the expulsion from the natal group (Clarke & Zucker, 1989;

Clarke et al., 2007). In a non primate mammal, the fossa (*Cryptoprocta ferox*), external genitalia of immature females are characterized by peculiar specific masculine traits (including a prominent/elongated clitoris with spines), which progressively fade in adulthood. This "transient masculinization" (Hawkins et al., 2002) has been tentatively interpreted as an advantage for the young females, who during their juvenile dispersal phase, may benefit from mimicking males, decreasing the risk of both sexual harassment by males (annual estrus is brief, and females are dispersed) and attacks by territorial adult females. If further studies would support *S. apella* "transient male mimicry" what would the female advantage be? In social primates, the presence and appearance of external genitalia may affect how others interact with infants and juveniles, as for example, in rhesus macaques whose male infants receive more genital inspection and less restriction than females (Dixon, 2012) In tufted capuchins, a mothers' biased behavior toward male infants, has never been described. During affiliative and playful interactions with both immature and adult individuals of both sexes, however, immature females have been observed erecting the clitoris, seemingly enhancing genital mimicry. Erection of the clitoris has never been observed in adult females (Fragaszy et al., 2004; M. C., personal observation). Nevertheless, direct evidence for a social function remains lacking.

Quantitative descriptions of patterns of clitoral hypertrophy (elongation) in tufted capuchins at different ages by mean of ontogenetic allometry, as well as comparisons with other species, revealed an interspecific variability potentially useful for both identifying different patterns of hypertrophy (e.g., *Ateles* spp, *L. catta*, *M. mulatta*) and hypothesizing diversified causal mechanisms, which, in turn, would possibly translate into different functional hypotheses. At the intraspecific level, future research should focus more on variability in clitoral size by collecting systematic quantitative measurements on a large sample to obtain normative data mandatory to disentangle likely functional hypotheses.

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