



# Same-sex and immature sexual behaviour repertoire in a wild group of robust capuchin monkeys

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**Abstract** – In primates, same-sex and immature sexual behaviour is widespread and can include mounting and genital presentation. These patterns can be observed in multiple social contexts and across all ages, and can serve functions such as appeasement, reconciliation, practice and dominance assertion. In this study, we investigated same-sex and immature sexual behaviour in a group of robust capuchins (*Sapajus nigritus*) living in an Atlantic forest fragment and urban areas. We predicted that in order to practice sex, sexual behaviour in same-sex dyads and/or dyads that included immatures would resemble the adult heterosexual repertoire for solicitation through courtship displays, mounts and post-copulatory display. We also predicted that immature individuals would engage more frequently than adults in sexual interactions, in order to practice sex. We conducted all-occurrence observations of sexual behaviour in the study group (28 individuals: four adult males, one sub-adult male, eight adult females, eight juveniles and seven infants) from September 2016 to August 2017. Sexual interactions that included at least one immature individual in the dyad and/or occurred between individuals of the same sex were infrequent ( $N = 52$ , 0.13 interactions/hour), but much more frequent than heterosexual sexual interactions between adults in the group ( $N = 4$ , 0.01 interactions/hour). The same-sex and immature sexual repertoire resembled the described heterosexual patterns for the same species from the literature. Individuals displayed solicitation behaviours in “one-way courtship”, usually followed by a two-way courtship and then mounts, but post-copulatory behaviour was never observed. Except for the alpha male, all age-sex classes engaged in sexual interactions in same-sex dyads or in dyads that included immature individuals. We found no difference in frequency of participation across age classes, however, male-male dyads engaged more frequently in sexual interactions and may be practicing sex and courtship behaviours. Mounts are unlikely to be a form of dominance assertion as the alpha male did not participate, subordinate adult males did not engage in mounts with other subordinate adult males, juveniles mounted adult males and *vice versa*, and there were mount switches (taking turns as mounter and mountee) regardless of the initial mounter’s age. Contrary to the post-conflict context observed in *Cebus*, most mounts in this study were preceded by play. Combining our study with additional evidence for the genus, same-sex mounts and mounts that include immatures seem to occur most commonly in affiliative contexts within *Sapajus*. Sexual behaviour functions in *Sapajus* require additional investigation, especially among adult males and juveniles of both sexes.

**Keywords** – courtship, display, mount, Platyrrhini, solicitation.

## Introduction

In several primate taxa, behavioural patterns commonly associated with reproductive sexual behaviour are also displayed by non-reproductive dyads in various social contexts (MacFarlane and Vasey, 2016; Vasey, 1995; Dixson, 2010, 2012). Although non-reproductive sexual behaviours may have important functions for heterosexual adult individuals, hereafter we are describing sexual interactions and their functional implications for same-sex dyads and dyads that include immature individuals. These patterns can take the form of mounting and genital contact, presentation and inspection, and are associated with contexts such as post-conflict, greeting and play (Leca *et al.*, 2002; Dixson, 2012). Among primate taxa, sexual behaviour can be expressed among all age-sex class dyads outside of a reproductive context and is hypothesized to have adaptive functions for individuals of all ages (Wrangham, 1993; Vasey, 1995; Dixson, 2012).

Sexual behaviour that includes immature individuals and/or same-sex dyads is especially well documented in cercopithecines and apes. For these taxa, individuals participate in sexual behaviour already during infancy. Infant Japanese macaques (*Macaca fuscata*) begin mounting their mothers or other female kin in an incomplete mounting pattern (Dixson, 2012; Gunst *et al.*, 2013), and over time display patterns of sexual solicitation, practicing to learn effective sexual solicitation (Gunst *et al.*, 2013). Immature (infant, juvenile and adolescent) gorillas, chimpanzees and bonobos display an extensive sexual repertoire, engaging in dorso-ventral and ventro-ventral thrusting as well as genital massage, oral sex and mouth kissing (Nadler, 1986; Wrangham, 1993; de Waal, 1990; Furuichi *et al.*, 2013; Grueter and Stoinski, 2016). In chimpanzees and bonobos, the frequent participation of infants and juveniles in sexual interactions is hypothesized to function as practice in preparation for reproductive sex (de Waal, 1990; Wrangham, 1993). For adults, sexual behaviour can serve other functions; for example, free-ranging male Barbary macaques (*Macaca sylvanus*) mount other males to assert dominance, as explained by

the dominance assertion hypothesis, with dominant individuals usually mounting subordinates (Faraut *et al.*, 2015). In the same way, dominant individuals commonly mount subordinates in captive groups of *Macaca mulatta*, *Macaca nemestrina* and *Macaca arctoides* (Maestripieri, 2005). In these groups, genital presentation and touching genitals are performed in the opposite direction, by subordinate individuals to dominant ones (Maestripieri, 2005). Furthermore, sexual behaviour is used by individuals in communication, as associated with consolation, reconciliation and appeasement (de Waal, 1990; Wrangham, 1993; Hohmann and Fruth, 2000; Clay and de Waal, 2014), and exchange of resources such as meat (Gomes and Boesch, 2009) and social benefits (e.g., grooming and protection) (Wrangham, 1993).

Evidence for same-sex and immature sexual interactions is less common for Platyrrhini; however, some behaviours and functions are described within this infraorder. Genital presentations are common in Callitrichinae (Fleagle, 2013; Wang *et al.*, 2019) and occur during agonism in marmosets (*Callithrix* spp.; Moynihan, 1970; Dixson, 2012) and as part of friendly displays in tamarins (*Saguinus geoffroyi*; Moynihan, 1970). Mounting behaviour among same-sex adults and immatures also has been observed in these taxa (Moynihan, 1970; Rothe, 1975). In male-male dyads of spider monkeys, *Ateles geoffroyi*, individuals have been observed occasionally to stimulate the partner's genitals with hand, mouth or feet during embraces (Schaffner *et al.*, 2012), as well as to perform mounts with anal intromission (Busia *et al.*, 2018), however, mount functions were not explored. Same-sex and immature sexual behaviour for the Cebinae (capuchin monkeys and squirrel monkeys) is better described, and mounts and mount functions in the group more closely resemble what is observed among catarrhine primates. Male and female squirrel monkeys (*Saimiri sciureus*) exhibit genital display postures along with penile and clitoral erections among same-sex dyads (Dixson, 2012), as well as mount and solicitation behaviours across age-classes (Talmage-Riggs and Ansel, 1973) and during play between

males (Ploog *et al.*, 1963). Same-sex sexual interactions in squirrel monkeys closely resemble heterosexual patterns (Talmage-Riggs and Ansel, 1973) and displays can be a method to communicate dominance or in other cases, an affiliative behaviour (Ploog *et al.*, 1963, Dixson, 2012).

In white-faced capuchins (*Cebus imitator*), a large proportion of the sexual behaviour observed is not reproductive and there is frequent participation of immatures in sexual interactions:  $0.0035 \pm 0.0052$  mounts/hour for adult heterosexual dyads and  $0.0059 \pm 0.0151$  for same-sex dyads and dyads that included immatures in Manson *et al.* (1997). Gracile capuchin males (*Cebus* spp.) have been documented to mount each other after conflicts for reconciliation (Leca *et al.*, 2002) and during other socially tense situations such as during coalition formation attempts and unsettled social relationship periods (Manson *et al.*, 1997; Leca *et al.*, 2002). In robust capuchin monkeys (*Sapajus* spp.) sexual practice has been observed in same-sex and/or immature dyads (Matheson *et al.*, 1996; Carosi and Visalberghi, 2002; Lynch, 2008; Back *et al.*, 2019; Rufo and Ottoni, 2020). In captivity, male-male mounts were observed during reunion displays (Matheson *et al.*, 1996), and adult-immature sexual behaviour was observed during affiliative interactions (Carosi and Visalberghi, 2002). In semi-free robust capuchin (*Sapajus* sp.) groups, sexual interactions with displays and/or mounts often involved juveniles (Back *et al.*, 2019; Rufo and Ottoni, 2020). In wild *Sapajus nigritus*, penile erections and mounting with thrusting were observed during scream-embrace displays (i.e., reunion displays) (Lynch, 2008), suggesting an affiliative nature to mounts in *Sapajus*.

Adult heterosexual behaviour has been described in detail for robust capuchin monkeys (Janson, 1984; Carosi and Visalberghi, 2002; Fragaszy *et al.*, 2004; Lynch, 2005). Typical sexual interactions begin with one-way courtship, most often initiated by a female who displays behaviours like grins, chest rubbing and head cocking towards a target male – this sequence can last hours or even days, and the

sexual initiator may not get a response from the partner (Carosi and Visalberghi, 2002). Eventually, two-way courtship may ensue, and male sexual response is characterized by a mutual gaze between the male and female, eyebrow raising by both individuals, and the female may continue to grin and emit a hoarse whine, especially during mounts (Carosi and Visalberghi, 2002). Mounting occurs as either single mount or multiple mount intromission, and can include mount switching, where the male and female take turns as mounter and mountee (Dewsbury and Pierce, 1989; Carosi and Visalberghi, 2002; Lynch, 2005). Males ejaculate after a single mount or after multiple mounts and never continue to copulate after ejaculation, the so called single ejaculation pattern (Carosi and Visalberghi, 2002). *Sapajus* sexual sequences can last up to a half an hour, and include several genus-specific behaviours linked to courtship (Carosi and Visalberghi, 2002). Post-copulatory display or post-ejaculatory courtship occurs when a sexual dyad continues to display strong interest in one another after a sexual interaction/ejaculation and emits behaviours similar to courtship; post-copulatory display has been associated with sperm competition (Carosi and Visalberghi, 2002; Carosi, 2005; Lynch, 2005).

In contrast, the frequency of same-sex and immature sexual interactions and the sexual behavioural repertoire in these dyads for robust capuchins have not yet been described. In this study, we describe the same-sex, immature-immature and adult-immature sexual repertoire in a wild black-horned capuchin monkey (*Sapajus nigritus*) social group living in an urban area with a semi-deciduous Atlantic forest fragment in Londrina, Brazil. We assessed the behavioural repertoire and age-sex class dyadic mounting frequency observed during sexual interactions. We expected that individuals would engage in sexual interactions in order to practice sex. Thus, sexual interactions would resemble the species' adult heterosex-

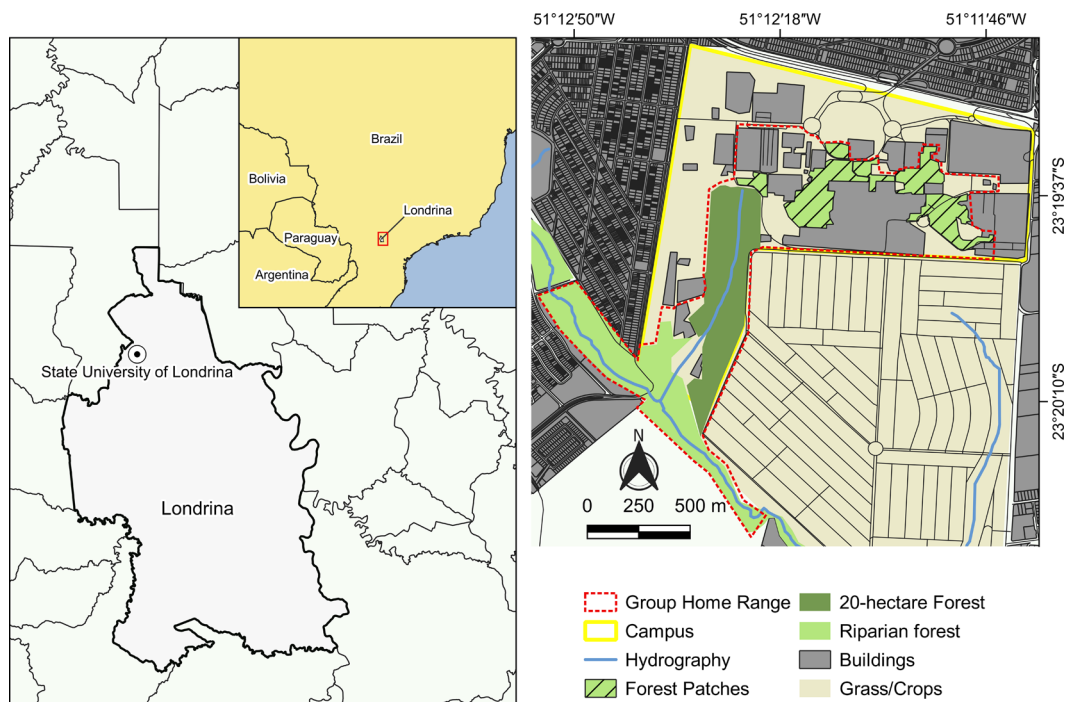
ual repertoire for solicitation, mount and post-copulatory display (Prediction 1). Also, immature individuals (infants, juveniles and sub-adults) would engage in same-sex and mature-immature mounts more frequently than adults (Prediction 2).

## Material and methods

### STUDY AREA AND SUBJECTS

This study was carried out at the campus of State University of Londrina, Londrina, Paraná state, Brazil, an urban area with a fragment of 20 hectares of semi-deciduous Atlantic Forest (23°19'45.2"S, 51°12'25.8"W) connected to a riparian forest (fig. 1). This fragment is a secondary forest that naturally regenerated within an agricultural matrix. The campus is a highly anthropized environment, formed by university buildings, a fragment of 20 hectares, forest patches in different successional stages, agricultural crops and pastures (fig. 1). During the study, this group comprised 28 individuals (four

adult males, one sub-adult male, eight adult females, eight juveniles and seven infants; age classes follow Fragaszy et al. (2004); table 1). Individuals were recognized by their natural markings and morphological characters. The group home range (approximately 100 hectares: riparian forest, forest fragment, university forest patches, crop and pasture areas) has remained similar since 1991 (Rocha, 1995). The group spent most of the time traveling in the small forest patches, the 20-hectare fragment and occasionally the riparian matrix. Animals foraged mostly on natural resources but also visited some buildings in the campus, and areas where they fed from trash cans and consumed human food. Humans sometimes provided natural and human food to the animals. There was often a high volume of human visitors on the campus interested in the capuchin monkeys, who sometimes exhibited agonistic displays, such as open-mouth threats and chases, towards humans.



**Figure 1.** Home range of the black-horned capuchin monkeys (*Sapajus nigritus*) within the campus of State University of Londrina, Londrina, Brazil and the neighboring riparian forest.

**Table 1.** Group composition of *Sapajus nigritus* during the study period. Infant (First year of life), Juvenile (1 year old+), Sub-adult male (5 years old), Adult male (6 years old+) and Adult female (5 years old+, or after conception).

Name	Sex	Age (2016–2017)
Alfa – the alpha male	Male	Adult
Hanks	Male	Adult
Dex	Male	Adult
Noah	Male	Adult
Harry	Male	Sub-adult
Brown	Female	Adult
Dixie	Female	Adult
Jolie	Female	Adult
Juca	Female	Adult
Zee	Female	Adult
Zoey	Female	Adult
Piper	Female	Adult
Lu	Female	Adult
Bailey	Female	Juvenile
Lucas	Female	Juvenile
Tico	Male	Juvenile
Chiquinho	Male	Juvenile
Jake	Male	Juvenile
Larry	Undetermined	Juvenile
João	Male	Juvenile
Billy	Male	Juvenile
Lau	Undetermined	Infant-Juvenile
Jazz	Male	Infant-Juvenile
Rob	Female	Infant-Juvenile
Oz	Female	Infant
Goo	Female	Infant
Feio	Female	Infant
Nikkie	Undetermined	Infant

#### DATA COLLECTION

Fieldwork was conducted from September 2016 to August 2017, three to five days per week from 0700 to 1900. During this period, because the monkeys tended to spread out widely and cluster in smaller feeding groups of individuals, we followed the group alternating among different feeding groups. In order to assess behavioural frequencies and perform a test of observability to verify whether we had the same opportunity to sample sexual behaviour in adults (males and females) and immature individuals (infants, juveniles and sub-adults) we conducted an adaptation of scan

sampling observations (Altmann, 1974) each month (Mean: 4.15 days/month). We scored the visible individuals and their activity (feeding, foraging, locomotion, affiliative, agonistic, self-directed, sexual and other) within a 15-minute scan followed by a 5-minute interval. During each 15-minute scan, MPL walked through the different feeding groups and scored each individual a single time for the behaviour it performed (e.g., playing, social or grooming in the affiliative category, self-grooming or resting in the self-directed category).

In order to sample the sexual behaviour in the group, we conducted an adapted form of all-occurrences observations (Altmann, 1974), since we were unable to maintain contact with all group members distributed in feeding groups. We collected data for all visible sexual interactions, including interactions between dyads of all sex-age classes. We began to sample the dyad after any sign of sexual behaviour, including during play, close proximity, grooming and agonistic episodes. We observed the dyad for the entire duration of the sexual interaction, after it began with a solicitation or mount (i.e., dorso-ventral mount with thrusting), and we recorded the behaviours on video (.mov, 720p–1080p) until the individuals engaged in non-sexual behaviours. It was not possible to verify intromission or ejaculation. For categorization and definition of behaviours during solicitation, mounts and post-copulatory display we adapted the ethograms of Carosi and Visalberghi (2002) and Fragaszy *et al.* (2004) (see table 2 for sexual behaviours that were observed in this study).

For each observed sexual interaction, we recorded the dyads' identity, sex and age composition, behaviours performed, potentially including a variety of solicitation behaviours, mounts and post-copulatory behaviours (table 2), and the sexual interaction duration in minutes. We also noted the behavioural context dyads were engaged in before they interacted sexually. These contexts included affiliative, agonistic, foraging, locomotion, play and vigilance.

**Table 2.** Behaviours observed during same-sex and immature sexual interactions for *Sapajus nigritus*.

Interaction stage	Behaviour	Definition	
Solicitation		Prior to the mount, “A” actively displays to “B” one or more of the behaviours described below. Usually known as <i>One-way courtship</i> .	
	Genital display	“A” spreads legs in front of “B” while his penis is erect and highly visible. “A” often performs <i>Belly or chest rubbing</i> .	
	Head cocking or tilting	The head is tilted to one side and changes side every few seconds.	
	Sitting or lying aside	“A” adopts a sitting or lying posture in close proximity to the sexual partner.	
	Eyebrow raising	Eyebrows are raised up and backwards. The fur in the crown is flattened and the fur in the forehead appears paler. Observed within solicitation and during the mount.	
	Grin	The corners of the mouth are retracted, baring some teeth while the jaw is closed. Observed within solicitation and during the mount. Usually accompanied by <i>Hoarse whine</i> .	
	Belly or chest rubbing	Hand or hands are gently moved up and down or lie still on the chest or belly fur.	
	Dorso-ventral embrace	Dorso-ventral contact between two individuals in which both interactors stand still together, in a relaxed posture and there is no thrusting. <i>Dorse-ventral embrace</i> is also observed during play.	
	Nuzzling	“A” gently and quickly contacts the body of “B” with the nose and/or mouth.	
	Tense arms	“A” moves one or both arms towards “B”, without touching “B”.	
Two-way courtship		After “A” solicits “B”, “B” responds to “A” with one or more solicitation behaviours.	
	Mutual gaze	Mutual eye contact between interactors during several seconds. Involves <i>Eyebrow raising</i> .	
	Mount		Dorso-ventral mount with thrusting, usually preceded by solicitation. Behaviours observed during mounts are described below.
		Hoarse whine	A repeated vocalization that is similar to a whistle or a “high frequency, low amplitude descending call”.
		Single mount	Mounter and mountee do not switch roles and there is no pause in the mount during the interaction.
Mount switch		Mounter and mountee switch roles during the mount series.	
Multiple mount	<i>Mount switch</i> or the same individual mounting again after brief pause.		

## STATISTICAL ANALYSES

For the purpose of performing the test of observability of age-sex classes, we compared the number of visibility records for adult males, adult females, and immatures to the expected number of visibility records based on overall group composition with a Chi-Squared test. We conducted a *post-hoc* test with a Bonferroni correction to verify which if any age-sex class differed from expected.

In order to compare adult and immature sexual interaction frequency, we calculated

the expected proportion of interactions for each age-class combination based on group composition. The frequency was based on a random model in which it was equally likely for any dyad, regardless of age-class-combination, to interact (table 3). We then calculated the expected frequency of interactions among adults, adult-immature and immature-immature dyads. We compared the observed frequency between adults, adult-immature and immature-immature dyads with expected frequency based on the calculated proportions with

**Table 3.** Random model for the expected proportion of sexual interactions of dyads of all age-classes in which individuals interact at the same frequency.

Age class	Adult Males (N = 4)	Adult Females (N = 8)	Immatures (N = 16)
Adult Males	0.016	0.085	0.169
Adult Females	–	0.074	0.339
Immatures	–	–	0.317

**Table 4.** Random model for the expected proportion of sexual interactions of dyads of all sex-classes and undetermined sex-class individuals in which individuals interact at the same frequency.

Sex class	Males (N = 11)	Females (N = 14)	Undetermined (N = 3)
Males	0.145	0.407	0.087
Females	–	0.241	0.111
Undetermined	–	–	0.008

a Chi-Squared test. In order to compare the interaction frequency among sex-classes, the same analysis was conducted with male-male, male-female and female-female dyads, and dyads with a non-identified individual (table 4). In these analyses, we verified which classes differed from the expected with *post-hoc* comparisons with a Bonferroni correction.

We compared the 1. number of distinct solicitation behaviours (from the list in table 2) in sexual interactions that began with solicitation, 2. number of distinct sexual behaviours (from the list in table 2) in all sexual interactions and 3. duration of interactions between dyads of particular age classes (same-sex adults, adult-immature and immature-immature) and sex-classes (male-male, male-female and female-female) with Kruskal-Wallis tests. When significant differences were indicated by the Kruskal-Wallis test, we conducted a Dunn's test with a Bonferroni correction to evaluate which groups differed. Interactions with unknown sex identification of one or both individuals (N = 6) were excluded from sex-class dyad comparisons.

In order to determine whether same-sex and immature sexual interactions were more likely

to occur during certain behavioural contexts, we compared the frequency of sexual interactions in the behavioural contexts in which interactions were observed to the expected frequencies based on the frequencies of those behaviours within all scan sampling observations (for example, did dyads engage in sexual interactions in an agonistic context more frequently than expected). For this analysis, we conducted a Fisher's exact test with a *post-hoc* comparison with a Bonferroni correction to verify the behavioural contexts in which frequencies differed from the expected. All analyses were done with a significance level at  $p < 0.05$ .

## Results

We followed the group for a total of 396 h 54 m and recorded 182 h 45 m of scan sampling. From the total 7152 records of individuals from scans, 3494 were for immatures, 1579 for mature males and 2079 for mature females. During the fieldwork, there was a bias in observability of different age-sex classes. Adult males were generally observed more frequently than expected (*post-hoc, adjusted*  $p < 0.0001$ ) and immatures observed less frequently than expected (*post-hoc, adjusted*  $p < 0.0001$ ), while females were observed at the expected frequency (*post-hoc, adjusted*  $p = 1$ ; Chi-squared test:  $\chi^2 = 166.09$ ,  $df = 2$ ,  $p < 0.0001$ ).

### FREQUENCY OF SEXUAL INTERACTIONS BY AGE AND SEX-CLASS

We observed a total of 56 sexual interactions (0.14 interactions/hour), of which 52 interactions were by same-sex adult, adult-immature, or immature-immature dyads (0.13 interactions/hour) and four were by adult heterosexual dyads (0.01 interactions/hour). We recorded solicitation and mount behaviours, however post-copulatory behaviour was never observed as part of sexual interactions by same-sex dyads and/or dyads including at least one immature individual (table 2). Regarding adult heterosexual interactions, all four observations were between the alpha male and adult females. The alpha male was never observed as either

**Table 5.** Expected frequency (and proportion) of sexual interactions in adult-adult, adult-immature, and immature-immature dyads.

	Adult-adult dyads	Adult-immature dyads	Immature-Immature dyads	Total
Expected frequency and proportion	9.8 (0.175)	28.45 (0.508)	17.75 (0.317)	56 (1)
Observed frequency and proportion	6 (0.107)	20 (0.357)	30 (0.536)	56 (1)

**Table 6.** Expected frequency (and proportion) of sexual interactions in male-male, male-female, female-female and undetermined-sex dyads.

	Male-male dyads	Male-female dyads	Female-female dyads	Undetermined dyads*	Total
Expected frequency and proportion	8.15 (0.145)	22.81 (0.407)	13.48 (0.241)	11.56 (0.206)	56 (1)
Observed frequency and proportion	16 (0.518)	16 (0.286)	5 (0.089)	6 (0.107)	56 (1)

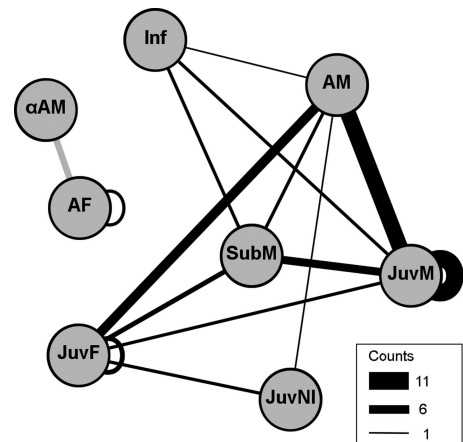
\* Undetermined dyads = Dyads with at least one individual of undetermined sex;  $p$ -value = 0.0630.

mounter or mountee in sexual interactions with same-sex partners or sexual interactions with immatures.

In terms of sexual interaction frequency by age class, adult dyads participated in six interactions (four adult heterosexual and two female-female interactions, 10.7%), adult-immature dyads in 20 interactions (35.7%) and immature-immature dyads in 30 interactions (53.6%). Based on our random model, individuals engaged in sexual interactions at the expected frequency (Chi-squared test:  $\chi^2 = 5.5303$ ,  $df = 2$ ,  $p = 0.0630$ ; table 5).

Regarding sex-class participation, male-male dyads ( $N = 19$ , 51.8%) engaged in sexual interactions more often than expected (*post-hoc*, *adjusted*  $p = 0.0002$ ) while male-female ( $N = 16$ , 28.6%; *adjusted*  $p = 1$ ), female-female ( $N = 5$ , 8.9%; *adjusted*  $p = 0.2469$ ), and undetermined sex dyads ( $N = 6$ , 10.7%; *adjusted*  $p = 1$ ) engaged in sexual interactions at the expected frequency (Chi-squared test:  $\chi^2 = 18.548$ ,  $df = 3$ ,  $p = 0.0003$ ; table 6).

Among immature-immature dyads, the most frequent dyads were two juvenile males ( $N = 11$ , 21.1% of the sexual interactions), and a sub-adult male and juvenile male ( $N = 5$ , 9.6%), but sexual interactions were observed among all immature age-sex class combinations (shown in fig. 2). Among adult-immature dyads, all dyads were formed by a subordinate adult male and



**Figure 2.** Observed frequency of sexual interactions in *Sapajus nigritus* among age-sex classes.  $\alpha$ AM = alpha adult male, AM = adult male, AF = adult female, SubM = sub-adult male, JuvM = juvenile male, JuvF = juvenile female, JuvNI = juvenile of unidentified sex and Inf = infant. Adult heterosexual dyads are connected with light grey lines and other dyads are connected with black lines.

an immature individual; the immature individuals were mostly juvenile males ( $N = 10$ , 19.2%) and juvenile females ( $N = 6$ , 11.5%). Subordinate adult males also engaged in sexual interactions with sub-adult males ( $N = 2$ , 3.8%), an infant female, and a juvenile of unidentified sex (shown in fig. 2; Sexual dyadic interactions observed, individuals and age-sex-classes are available in the supplementary table S1).



**Table 7.** Number of sexual interactions by *Sapajus nigritus* dyads of different age-class categories that included particular solicitation and mount behaviours. S-S A-A = same-sex adult individuals, A-I = adult-immature dyads, I-I = immature-immature dyads.

Behaviour	S-S A-A (N = 2)	A-I (N = 20)	I-I (N = 30)	Number of interactions in which this behaviour was observed (Total events = 52)
Solicitation behaviours				
Solicitation	1	16	22	39
Eyebrow raising	1	16	20	37
Sitting or lying aside	1	14	20	35
Mutual gaze	1	6	5	12
Two-way courtship	1	6	5	12
Genital display	0	5	6	11
Head cocking/tilting	1	5	5	11
Grin	0	5	6	11
Dorso-ventral embrace	0	4	6	10
Belly or chest rubbing	0	3	5	8
Nuzzling	0	3	5	8
Tense arms	0	3	4	7
Mount behaviours				
Eyebrow raising	2	20	28	50
Grin	2	14	19	35
Multiple mount	0	8	14	22
Mount switch	0	8	14	22
Hoarse whine	1	9	9	19

#### SOLICITATION AND MOUNT BEHAVIOURS IN SEXUAL INTERACTIONS BY AGE AND SEX-CLASS

Sexual interactions could either begin with solicitation behaviours (considered ‘courtship behaviours’ in heterosexual dyads) or start directly with a mount. For five of the sexual interactions all ten solicitation behaviours were observed (see table 7), and in contrast, in 13 of the sexual interactions no solicitation behaviours were observed before the mount. When solicitations were observed, *Eyebrow raising* was the most commonly displayed solicitation behaviour, followed by *Sitting/Lying aside* and *Mutual gaze*. During mounts, *Eyebrow raising* and *Grin* were the most displayed behaviours (table 7).

Mounts could be preceded by solicitations in all sex-class combinations but *Genital display*, *Grin*, *Dorso-ventral embrace* and *Nuzzling* were observed exclusively among male-male dyads. *Mutual gaze*, *Two-way courtship*, *Head cocking/tilting*, *Belly or chest rubbing* and

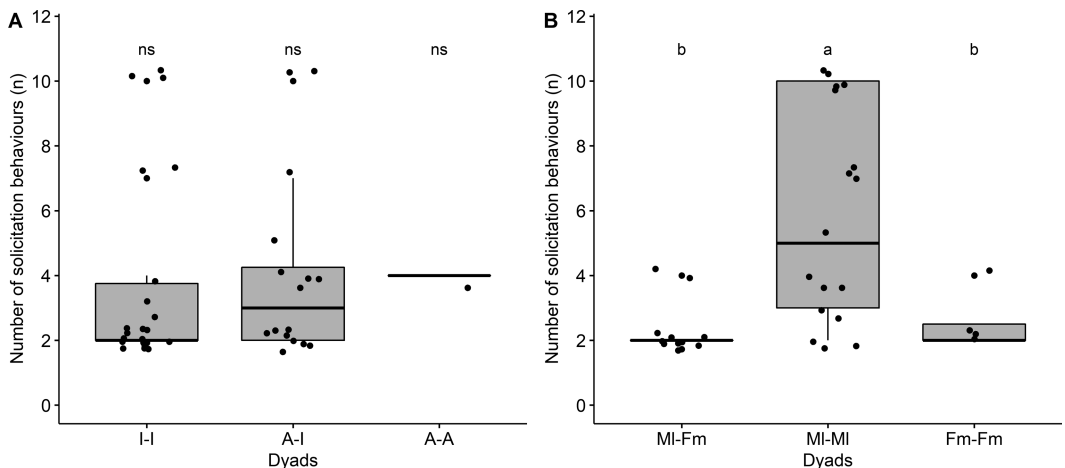
*Tense arms* were mainly observed before male-male mounts, with single or no occurrences in male-female and female-female interactions. During mounts, male-female dyads did not engage in *Multiple mount* or *Mount Switch*, and the *Hoarse-whine* vocalization was observed almost exclusively in male-male dyads (table 8).

During solicitations, male-male dyads (median = 5 (interquartile range = 3–10)) performed a significantly higher number of distinct behaviours than male-female (2(2–2)) and female-female dyads (2(2–2.5); Kruskal-Wallis:  $\chi^2 = 13.975$ ,  $df = 2$ ,  $p = 0.0009$ ; Dunn’s test: MI-MI and Fm-Fm,  $Z = -2.1780$ , *adjusted p* = 0.0441; MI-MI and MI-Fm,  $Z = -3.5275$ , *adjusted p* = 0.0006; MI-Fm and Fm-Fm,  $Z = 0.2073$ , *adjusted p* = 1; fig. 3B). However, the number of distinct behaviours in solicitations did not differ significantly across age-classes (Kruskal-Wallis:  $\chi^2 = 1.0918$ ,  $df = 2$ ,  $p = 0.5739$ ; fig. 3A).

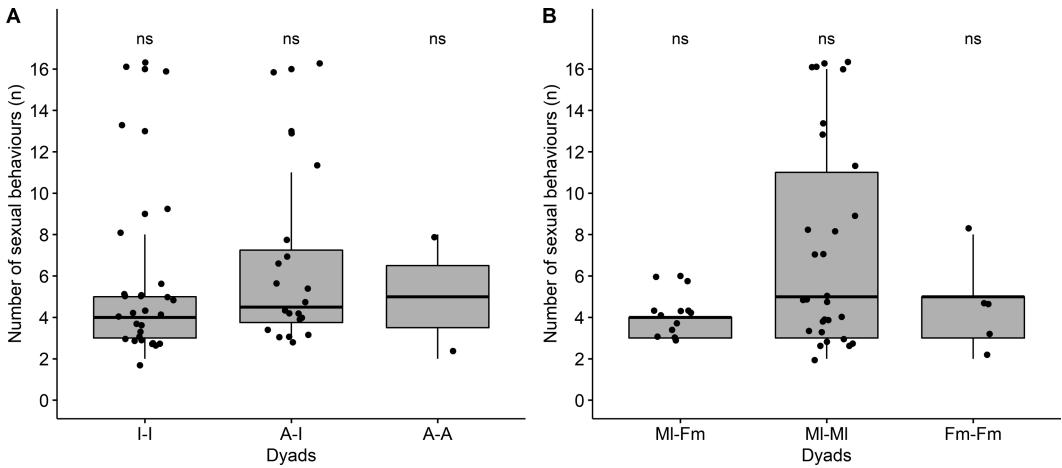
The number of solicitation and mount behaviours displayed during sexual interactions

**Table 8.** Number of sexual interactions by *Sapajus nigritus* dyads of different sex-class categories that included particular solicitation and mount behaviours. MI-Fm = Male-female same-sex and immature dyads, MI-MI = male-male dyads, Fm-Fm = female-female dyads.

Behaviour	MI-Fm (N = 12)	MI-MI (N = 29)	Fm-Fm (N = 5)	Number of interactions in which this behaviour was observed (Total events = 46)
<b>Solicitation behaviours</b>				
Solicitation	12	17	4	33
Eyebrow raising	12	15	4	31
Sitting or lying aside	12	13	4	29
Mutual gaze	1	10	1	12
Two-way courtship	1	10	1	12
Genital display	0	11	0	11
Head cocking/tilting	1	9	1	11
Grin	0	11	0	11
Dorso-ventral embrace	0	10	0	10
Belly or chest rubbing	1	7	0	8
Nuzzling	0	8	0	8
Tense arms	1	6	0	7
<b>Mount behaviours</b>				
Eyebrow raising	12	27	5	44
Grin	7	24	2	33
Multiple mount	0	18	2	20
Mount switch	0	18	2	20
Hoarse whine	1	18	0	19



**Figure 3.** Median number of different solicitation behaviours observed in same-sex and immature sexual interactions that included solicitation for *Sapajus nigritus* in A) immature-immature (I-I), adult-immature (A-I) and adult female (A-A) dyads, and B) male-female (MI-Fm), male-male (MI-MI) and female-female (Fm-Fm) dyads. Letters represent significant differences among groups, ns = non-significant.



**Figure 4.** Median number of different sexual behaviours observed in same-sex and immature sexual interactions for *Sapajus nigritus* in A) immature-immature (I-I), adult-immature (A-I) and adult female (A-A) dyads, and B) male-female (MI-Fm), male-male (MI-MI) and female-female (Fm-Fm) dyads. Ns = non-significant.

was variable: (median = 3 (interquartile range 4–7)). Five interactions included all 16 behaviours, and these were all within male-male dyads. However, we found no significant difference in the number of distinct sexual behaviours in interactions for adult-immature (4.5(3.75–7.25)), adult female (5(3.5–6.5)), and immature-immature dyads (4(3–5); Kruskal-Wallis:  $\chi^2 = 0.8512$ ,  $df = 2$ ,  $p = 0.6534$ ; fig. 4A), or for male-male (5(3–11)), male-female (4(3–4)) and female-female dyads (5(3–5); Kruskal-Wallis:  $\chi^2 = 3.9322$ ,  $df = 2$ ,  $p = 0.14$ ; fig. 4B).

#### DURATION OF SEXUAL INTERACTIONS BY AGE AND SEX-CLASS

Sexual interactions lasted for a few seconds up to ten minutes. The median duration of sexual interactions was similar for age-classes (Kruskal-Wallis:  $\chi^2 = 13.095$ ,  $df = 2$ ,  $p = 0.9366$ ; fig. 5A). Regarding the duration of sexual interactions in sex-class dyads, male-male interactions (median = 2 minutes (interquartile range 1–8 minutes)) lasted longer than male-female interactions (1(1–1)) but neither of these differed significantly from female-female dyads (1(1–2); Kruskal-Wallis:  $\chi^2 = 10.933$ ,  $df = 2$ ,  $p = 0.0043$ ; Dunn's test: MI-MI and MI-Fm,  $Z = -3.2818$ , *adjusted p* = 0.0015; MI-MI and Fm-Fm,  $Z = -1.0749$ , *adjusted*

**Table 9.** Number of same-sex and immature sexual interactions by *Sapajus nigritus* in which adult and immature individuals were the initial mounter, mount-tee and the switched mounter. The initial mounter is in the first column and the subset of interactions in which there were mount switches are in parentheses.

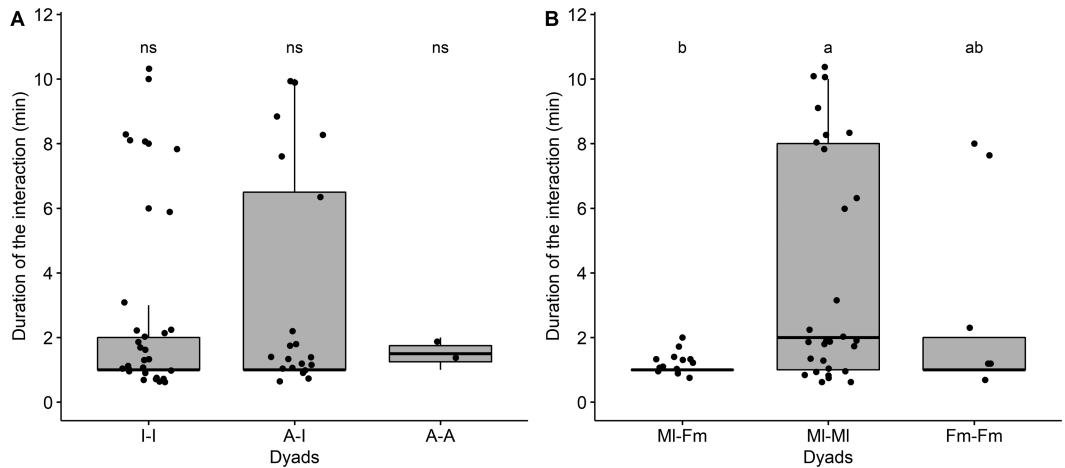
Initial mounter	Initial mountee	
	Adult	Immature
Adult	2 (0)	13 (6)
Immature	7 (2)	30 (14)

$p = 0.4236$ ; MI-Fm and Fm-Fm,  $Z = 1.1384$ , *adjusted p* = 0.3824; fig. 5B),

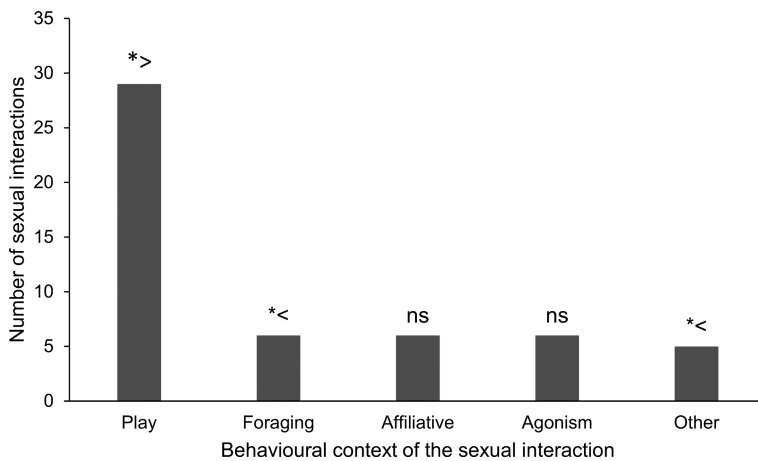
During sexual interactions, individuals could engage in single or multiple mounts. In all observed multiple mounts individuals changed roles at some point during the interaction. Multiple mounts and mount switches generally occurred in adult-immature (40% of the interactions) and immature-immature dyads (47%) but were not observed in the adult female dyads (table 9).

#### BEHAVIOURAL CONTEXTS OF SEXUAL INTERACTIONS

Regarding the behavioural context of interactions, same-sex and immature sexual interactions were most frequently observed during play (29, 55.8%). Interactions were also



**Figure 5.** Median duration of same-sex and immature sexual interactions for *Sapajus nigritus* in A) immature-immature (I-I), adult-immature (A-I) and adult female (A-A) dyads, and B) male-female (MI-Fm), male-male (MI-MI) and female-female (Fm-Fm) dyads. Letters represent significant differences among groups, ns = non-significant.



**Figure 6.** Same-sex and immature sexual interactions observed during play, foraging, affiliative, agonism and other (locomotion and vigilance) behavioural contexts in *Sapajus nigritus*. \* $\geq$  higher than expected frequency ( $p < 0.05$ ), \* $\leq$  less than expected frequency ( $p < 0.05$ ), ns = non-significant.

recorded during foraging (6, 11.5%), affiliative behaviour (6, 11.5%; i.e., grooming and alloparental care), agonism (6, 11.5%), and other behavioural contexts (5, 9.6%; i.e., locomotion and vigilance; shown in fig. 6). Based on scan sampling data, the most frequent among the cited behaviours was foraging (58%), followed by others (32%; i.e., locomotion and vigilance), play (5%), grooming and alloparental care (3%), and agonism (2%). Individuals

engaged in sexual behaviour during play (*post-hoc*, *adjusted*  $p < 0.0001$ ) more often than expected, and in the expected frequency during affiliative behaviours (*adjusted*  $p = 0.269$ ) and agonism (*adjusted*  $p = 0.112$ ). Sexual interactions during foraging (*adjusted*  $p < 0.0001$ ) and others (*adjusted*  $p = 0.0366$ ) occurred at a less than expected frequency (Fisher's test:  $n = 52$ ,  $p < 0.0001$ ).

We synthesized the main findings of this study regarding the characteristics of same-sex

**Table 10.** Main findings for characteristics of sexual interactions in same-sex dyads and dyads including immature individuals in this study.

Sexual behaviour topic	Findings
Same-sex and immature participation in sexual behaviour	Sexual behaviour was observed in almost every age and sex combination in the group, including male-male, female-female, and adult-immature dyads. However, the alpha male was never observed in sexual interactions with individuals other than adult females. Subordinate adult males did not engage in sexual behaviour with each other but frequently interacted sexually with male and female juveniles.
Sexual behaviour frequency	Male-male dyads engaged in sexual behaviour more frequently than male-female or female-female dyads.
Similarity to adult heterosexual sexual interactions	Solicitations and mounts in sexual interactions for same-sex dyads and dyads including immature individuals were similar to those observed during adult heterosexual behaviour. However, post-copulatory displays were never observed during same-sex or immature sexual interactions in this study.
Solicitations	Most sexual interactions for same-sex dyads and dyads including immature individuals began with solicitation behaviours. Male-male dyads performed a higher number of distinct behaviours during solicitations, and several solicitation behaviours were observed exclusively in male-male dyads ( <i>Genital Display</i> , <i>Grin</i> , <i>Dorso-ventral embrace</i> and <i>Nuzzling</i> ).
Mounts	Same-sex and immature dyads performed multiple mounts and mount switches, interchanging mounter and mountee roles during the interactions.
Duration of interaction	Sexual interactions for same-sex dyads and dyads including immature individuals lasted from a few seconds to ten minutes, as seen in adult heterosexual interactions.
Behavioural context in which individuals engaged in sexual behaviour	Play behaviour was the most commonly observed context (56%) before sexual interactions among same-sex dyads and dyads including immature individuals, and individuals displayed sexual interactions in a play context more frequently than expected based on the frequency of play in the study. Sexual interactions were also observed in contexts of affiliative behaviour (11.5%) and agonism (11.5%) at the expected frequency, and foraging (11.5%) and other behavioural contexts (9.6%) in less than expected frequency.

and sexual behaviour with immatures within the following table (table 10).

## Discussion

Same-sex and immature sexual repertoire for black-horned capuchins *Sapajus nigritus* observed in this study was similar to that described for heterosexual behaviour in robust capuchin monkeys (Carosi and Visalberghi, 2002; Fragaszy *et al.*, 2004; Matthews, 2012), as expected in our first prediction. Sexual interactions lasted from a few seconds, as described for male-male mounts in captivity (Rufo and Ottoni, 2020), to ten minutes, resembling the duration of heterosexual interactions in the wild (Janson, 1984). In our study, same-sex and immature dyads of black-horned capuchins displayed species-characteristic sexual solicitation

behaviours – a fundamental part of courtship – and mount behaviours, but post-copulatory display was absent. This is not unexpected, as most of the species-characteristic solicitation behaviours are also displayed by all age classes within affiliative contexts (Carosi and Visalberghi, 2002; De Marco and Visalberghi, 2007). A study on a semi-free ranging group described four male-male mounts in *Sapajus* sp.; these males displayed grins, whines and bared teeth before and during mounts (Rufo and Ottoni, 2020).

Despite being part of the heterosexual courtship repertoire in the genus, courtship behaviours such as *Touch-and-running*, *Frontal posture*, *Back posture*, *Backing into lap* and *Genital inspection* were not observed as part of sexual interactions for same sex dyads or dyads including at least one immature individual in this

study (Carosi and Visalberghi, 2002; Fragaszy *et al.*, 2004). It is likely that these behaviours are exclusive to heterosexual interactions instead of solicitation behaviours displayed both during non-sexual and sexual interactions. At least in this study, despite the similarity to the heterosexual behaviour, sexual behaviour among same sex and immature individuals did not include all the typical heterosexual sexual behaviours. On the other hand, the *Dorso-ventral embrace* behaviour has not been described previously in the heterosexual sexual repertoire, but was observed preceding several mounts in our study and elsewhere for *Sapajus nigritus* (Lynch, 2008). While we did not verify ejaculation in the study, it is likely that the age of interactants and swiftness of most interactions result in the absence of ejaculation, explaining the lack of the post-copulatory display, described for *Sapajus apella* as following a two-way courtship behaviour pattern after the occurrence of ejaculation (Carosi and Visalberghi, 2002). Post-copulatory display in black-horned capuchins has been hypothesized to be a form of sperm competition (Lynch, 2005) and in the case of same-sex and immature mounts it may not be expressed by the interactants, as there is no sperm competition.

In contrast to our second prediction based on the practice hypothesis, we found that sexual interaction frequency was not related to the age class composition of the dyad, as immature individuals did not participate significantly more than expected in sexual interactions. However, we found that male-male dyads were more likely to engage in sexual interactions. When solicitation behaviours were present in a sexual interaction, it was the male-male dyads that engaged in more complex solicitation (i.e., higher number of distinct solicitation behaviours) and in longer interactions. The behaviours *Genital display*, *Grin*, *Dorso-ventral embrace*, *Nuzzling*, *Mutual gaze*, *Two-way courtship*, *Head cocking/tilting*, *Belly or chest rubbing* and *Tense arms* were observed exclusively or almost exclusively prior to male-male mounts. Interestingly, initial sexual solicitation (i.e., one-way courtship) in heterosexual dyads in *Sapajus* is usually performed by

the female, and both male and female exchange several different solicitation behaviours in the two-way courtship (Carosi and Visalberghi, 2002). Thus, we might expect male-female dyads that include immatures to engage in similar interactions; however, complex solicitations were mainly observed among male-male dyads. Thus, sexual behaviour may be a form of practice for males in the species, even as subordinate adults.

During sexual interactions, males have the opportunity to coordinate the solicitation behaviours with a partner and combine them into a more complex arrangement, similar to the heterosexual courtship sequence. This was evidenced by the complex solicitations in male-male interactions. These practice opportunities can be particularly important for subordinate adult males, as adult females have the opportunity to practice solicitation and sexual behaviour every estrous period, while non-alpha male robust capuchins have limited opportunities for sexual interactions with females due to females' preference for the alpha male as sexual partner (Janson, 1984; Lynch, 2005). This would explain the frequent participation of subordinate adult males, the lack of participation by the alpha male, and the infrequent participation of adult females in same-sex and immature sexual interactions. It is relevant to note that even though there was a relatively small participation of adult females in mounts, juvenile females also participated in sexual interactions, suggesting there may a role for learning or practicing sexual interactions for young females in *Sapajus*.

Robust capuchin same-sex and immature sexual interactions seem to be most similar to mounts described for squirrel monkeys (*Saimiri*) as "Sexual Play", in which males engaged in same-sex mounts with or without penile erection after sexual solicitations (Ploog *et al.*, 1963). During "Sexual Play" mounts, there were mount switches and this behaviour was related to a relaxed mood in the squirrel monkey group (Ploog *et al.*, 1963). In our study, same-sex and immature sexual interactions were observed most frequently during

play, and rarely followed conflicts. The prevalence of sexual behaviour during play was unrelated to the frequent participation of immatures. We had greater observability of adult males and thus opportunities to sample sexual behaviour among several contexts. However, adult individuals engaged in sexual behaviour preferentially during specific affiliative contexts (i.e., play) and with juveniles. Same-sex and immature sexual behaviour in black-horned capuchins may not be a form of conflict resolution or reconciliation but instead have an affiliative function. While clasping and mounts are frequent forms of reconciliation in *Cebus* (Leca *et al.*, 2002), dyadic conflict frequency in *Sapajus nigritus* and rate of competition between males in *Sapajus* were not predictors of embrace (Lynch, 2008) or mount frequency (Matheson *et al.*, 1996). In black-horned capuchins male-male embrace and mount behaviours were mostly observed during subgroup and intergroup reunions and pointed out to act as a reinforcement of affiliative bonds for male dyads (Matheson *et al.*, 1996; Lynch, 2008). Like the mounts in our study, embraces and mounts in these other studies were generally observed among males (male-male embrace frequency: 42 out of 66 (64%) (Lynch, 2008); male-male mount frequency: 4 out of 4 (100%) (Matheson *et al.*, 1996)).

It is very unlikely that sexual interactions in our study functioned as a form of dominance assertion due to four potential factors. First, the dominant male never participated in same-sex sexual interactions. Second, subordinate male adults never engaged in sexual behaviour with other adults, suggesting that this behaviour is unrelated to setting or enforcing hierarchy status or appeasing subordinate adult males. Third, immatures took part in sexual interactions with immatures and adults as both initial mounters and initial mountees, as seen in wild white-faced capuchins (*Cebus capucinus*) (Manson *et al.*, 1997). Both immatures and male adults assumed both the mounter and mountee roles, often within the same interaction through mount switching. And fourth, mount switching occurred regardless of whether the immature or adult individual held the initial mounter

role. In male-male mounts in captivity, not only were *Sapajus* spp. subordinate males observed mounting dominants and beta males mounting alpha males, but also juveniles of both sexes mounted adults (Matheson *et al.*, 1996; Carosi and Visalberghi, 2002; Rufo and Ottoni, 2020). Thus, current data for robust capuchins argue against the dominance assertion hypothesis (see Oi, 1990 and Faraut *et al.*, 2015).

In black-horned capuchins, same-sex and immature sexual interactions resemble heterosexual courtship and mount behaviour, but post-copulatory display is absent. Male-male dyads engaged more frequently in more complex sexual behaviour interactions, therefore, this behaviour may be a form of sexual practice for males. Same-sex and immature sexual behaviour was mostly observed during play and, interestingly, even though the reconciliation function of mounts is clear for *Cebus*, the evidence here and elsewhere for its sister group *Sapajus* supports affiliative rather than conflict-related functions. While our study provides a group-wide analysis of sexual behaviour over a year-long period, same-sex and immature sexual behaviour functions in *Sapajus* still require further investigation in long-term studies to consider the interactors' rank relationships, kinship relationships, and the possibility of mounting for social bond formation, especially in adult males and in juveniles of both sexes.

### Statement of ethics

This research was noninvasive and observational only. The black-horned capuchin monkey study group was habituated to human presence and to the researchers. This study complied with the legal and ethical requirements of Brazil and the project was previously approved by the Animal Ethics Committee of the State University of Londrina (CEUA n. 12803.2016-74).

### Conflict of interest statement

Authors declare no conflict of interest involved in developing or publishing this study.

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## Author contributions

A.P.V.M., M.L.O. and M.P.L. conceived and designed the study. M.P.L. conducted the field work. E.A.F. conducted the analyses. E.A.F. and F.S.M.P. drafted the manuscript. J.W.L, M.L.O and A.P.V.M. supervised M.P.L., E.A.F. and F.S.M.P. and provided editorial advice, making critical content review. All authors discussed and gave final approval of the submitted version.

## Data availability statement

The data analysed during the current study are broadly included in the article and its supplementary material files. Further data can be requested from the corresponding author.

## Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.21988436>

## References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Back J, Suzin A, Aguiar L (2019). Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (Primates: Cebidae). *Zoologia* 36: 1–10. <https://doi.org/10.3897/zoologia.36.e30845>.

Busia L, Denice AR, Aureli F, Schaffner CM (2018). Homosexual behavior between male spider monkeys (*Ateles geoffroyi*). *Archives of Sexual Behavior* 47: 857–861. <https://doi.org/10.1007/s10508-018-1177-8>.

Carosi M, Visalberghi E (2002). Analysis of tufted capuchin (*Cebus apella*) courtship and sexual behavior repertoire: changes throughout the female cycle and female interindividual differences. *American Journal of Physical Anthropology* 118: 11–24.

Chevalier-Skolnikoff S (1974). Male-female, female-female, and male-male sexual behavior in the stump-tail monkey, with special attention to the female orgasm. *Archives of Sexual Behavior* 3: 95–116.

Clay Z, de Waal BM (2014). Sex and strife: post-conflict sexual contacts in bonobos. *Behaviour* 152: 313–334. <https://doi.org/10.1163/1568539X-00003155>.

De Marco A, Visalberghi E (2007). Facial displays in young tufted capuchin monkeys (*Cebus apella*): appearance, meaning, context and target. *Folia Primatologica* 78: 118–137.

de Waal FBM (1990). Sociosexual behavior used for tension regulation in all age and sex combinations among bonobos. In *Pedophilia* (Feierman JR, ed.), pp. 378–393. New York, Springer.

Dewsbury D, Pierce J (1989). Copulatory patterns of primates as viewed in broad mammalian perspective. *American Journal of Primatology* 17: 51–72. <https://doi.org/10.1002/ajp.1350170106>.

Dixson A (2010). Homosexual behavior in primates. In *Animal Homosexuality: a Biosocial Perspective* (Polani A, ed.), pp. 381–400. Cambridge, Cambridge University Press.

Dixson A (2012). *Primate Sexuality: Comparative Studies of Prosimians, Monkeys, Apes and Humans*. New York, Oxford University Press.

Faraut L, Northwood A, Majolo B (2015). The functions of non-reproductive mounts among male Barbary macaques (*Macaca sylvanus*). *American Journal of Primatology* 77(11): 1149–1157. <https://doi.org/10.1002/ajp.22451>.

Fleagle J (2003). *Primate Adaptation and Evolution*. San Diego, Academic Press.

Fragaszy DM, Visalberghi E, Fedigan LM (2004). *The Complete Capuchin: the Biology of the Genus Cebus*. Cambridge, Cambridge University Press.

Furuichi T, Connor R, Hashimoto C (2013). Non-conceptive sexual interactions in monkeys, apes, and dolphins. In *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies* (Yamagiwa J, Karczmarski L, eds.), pp. 385–408. Springer.

Gomes CM, Boesch C (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One* 4(4): e5116. <https://doi.org/10.1371/journal.pone.0005116>.

Grueter CC, Stoinski TS (2016). Homosexual behavior in female mountain gorillas: reflection of dominance, affiliation, reconciliation or arousal? *PLoS One* 11(5): e0154185. <https://doi.org/10.1371/journal.pone.0154185>.



- Gunst N, Leca JB, Vasey PL (2013). Development of sexual and socio-sexual behaviours in free-ranging juvenile male Japanese macaques (*Macaca fuscata*). *Behaviour* 150: 1225–1254. <https://doi.org/10.1163/1568539X-00003088>.
- Hohmann G, Fruth B (2000). Use and function of genital contacts among female bonobos. *Animal Behaviour* 60: 107–120.
- Janson CH (1984). Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). *Zeitschrift für Tierpsychologie* 65: 177–200.
- Leca JB, Fornasieri I, Petit O (2002). Aggression and reconciliation in *Cebus capucinus*. *International Journal of Primatology* 23: 979–998.
- Lynch JW (2005). Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigrilus*). *American Journal of Primatology* 67: 313–328.
- Lynch JW (2008). Scream-embrace displays in wild black-horned capuchin monkeys. *American Journal of Primatology* 70: 551–559.
- MacFarlane GR, Vasey PL (2016). Promiscuous primates engage in same-sex genital contact. *Behavioural Processes* 126: 21–26.
- Maestriepieri D (2005). Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*): use of signals in relation to dominance and social context. *Gesture* 5: 57–73.
- Manson JH, Perry S, Parish AR (1997). Nonconceptive sexual behavior in bonobos and capuchins. *International Journal of Primatology* 18: 767–786.
- Matheson MD, Johnson JS, Feuerstein J (1996). Male reunion displays in tufted capuchin monkeys (*Cebus apella*). *American Journal of Primatology* 40: 183–188.
- Matthews LJ (2012). Variations in sexual behavior among capuchin monkeys function for conspecific mate recognition: a phylogenetic analysis and a new hypothesis for female proceptivity in tufted capuchins. *American Journal of Primatology* 74(4): 287–298. <https://doi.org/10.1002/ajp.21004>.
- Moynihan M (1970). Some behavior patterns of Platyrrhine monkeys II. *Saguinus geoffroyi* and some other tamarins. *Smithsonian Contributions to Zoology* 28: 1–77.
- Nadler RD (1986). Sex-related behavior of immature wild mountain gorillas. *Developmental Psychobiology* 19: 125–137.
- Oi T (1990). Patterns of dominance and affiliation in wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in west Sumatra. *International Journal of Primatology* 11: 339–356.
- Ploog DW, Blitz J, Ploog F (1963). Studies on social and sexual behavior of the squirrel monkey (*Saimiri sciureus*). *Folia Primatologica* 1: 29–66.
- Rocha VJ (1995). *Dieta, ação sobre as sementes, padrão de atividade e área de vida de Cebus apella (Linnaeus, 1758) em três fragmentos florestais de tamanhos distintos na região de Londrina-PR*. Master's Thesis, Universidade Federal do Paraná.
- Rothe H (1975). Some aspects of sexuality and reproduction in groups of captive marmosets (*Callithrix jacchus*). *Zeitschrift für Tierpsychologie* 37: 255–273.
- Rufo HP, Ottoni EB (2020). Anecdotic observations of homosexual behaviour among male capuchin monkeys (*Sapajus* sp.). *Behaviour* 158: 89–97. <https://doi.org/10.1163/1568539X-bja10055>.
- Schaffner CM, Slater KY, Aureli F (2012). Age related variation in male-male relationships in wild spider monkeys (*Ateles geoffroyi yucatanensis*). *Primates* 53: 49–56. <https://doi.org/10.1007/s10329-011-0271-5>.
- Talmage-Riggs G, Ansel S (1973). Homosexual behavior and dominance hierarchy in a group of captive female squirrel monkeys (*Saimiri sciureus*). *Folia Primatologica* 19: 61–72.
- Vasey PL (1995). Homosexual behavior in primates: a review of evidence and theory. *International Journal of Primatology* 16: 173–204.
- Vasey PL, Rains D, VanderLaan DP, Duckworth N, Kovacovsky SD (2008). Courtship behaviour in Japanese macaques during heterosexual and homosexual consortships. *Behavioural Processes* 78: 401–407.
- Wang X, Lim BK, Ting N, Hu J, Liang Y, Roos C, Yu L (2019). Reconstructing the phylogeny of new world monkeys (*Platyrrhini*): evidence for multiple non-coding loci. *Current Zoology* 65: 579–588. <https://doi.org/10.1093/cz/zoy072>.
- Woods V, Hare B (2011). Bonobo but not chimpanzee infants use socio-sexual contact with peers. *Primates* 52: 111–116. <https://doi.org/10.1007/s10329-010-0229-z>.
- Wrangham RW (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature* 4: 47–79.