

Face-to-face interactions between mothers and female infants in wild bearded capuchin monkeys (*Sapajus libidinosus*)

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Abstract

Once considered uniquely human, mother–infant face-to-face interactions (FF) were observed in a few captive primates. In these studies, FF were correlated to physical contact suggesting a mechanism mediating proximity between mother and infant, as is the case for humans. We investigated this hypothesis in wild capuchin monkeys (*Sapajus libidinosus*) during the first year of life of eight female infants. Data were weekly focal-day videos of infants from which we recorded FF with mothers. We expected FF would increase with infants' age (as time in contact with mothers decreased) and would more likely occur in the absence of physical contact between the dyad. There was no effect of age in the proportion of interaction time spent in FF, nor in types of FF. A quarter of FF episodes occurred in the absence of physical contact between the dyad, and in most of them physical contact was resumed following the FF. Contrary to predictions, the stability in the first year, mainly when mothers–female infants were in contact, indicates that FF act primarily promoting opportunities for affective communication and intuitive care. However, we found some supportive evidence for the hypothesis that FF regulate proximity between mother and infant, mainly in resume physical contact.

KEYWORDS

attachment, development, intuitive care, maternal care, mother–infant interaction, mother–infant physical contact, primate infancy

1 | INTRODUCTION

Face-to-face interactions (FF) are an universal system of human parenting behavior (Keller, 2007) and one of the channels of early affective communication between mothers and their babies (Fogel, Messinger, Dickson, & Hsu, 1999; Tronick, 1989). From birth to childhood, mother and infant engage in FF through mutual gaze that are often preceded and accompanied by exaggerated particular patterns of crying, and facial expressions, kiss, and play (Fogel et al., 1999), that attract each other's attention and enhance the mutual engagement (Seidl de Moura et al., 2004). According to Beebe et al. (2018), FF communication is a dyadic system in which both partners contribute to exchange through a bidirectional co-regulation. There is

evidence that these interactions influence the infant physiological (Feldman et al., 2009) and emotional regulation (Feldman, 2007), induce a sense of agency (Keller & Greenfield, 2000; Murray, Fiori-Cowley, Hooper, & Cooper, 1996), and increase bonding and closeness between mother and infant (Feldman, 2012; Trevarthen, 1998).

FF between mothers and infants is actively performed in all human cultures, but the frequency in which mother and infant dyads engage in these interactions vary broadly according to the mother's experience, intrinsic characteristics of mother and infant, and their sociocultural surroundings. In sociocultural contexts where mothers prioritize face-to-face interactions in relation to physical contact, mutual gaze is thought to compensate for the early dyad physical separation (Hsu & Fogel, 2003; Keller, 2007; Morelli et al., 2017),

providing emotional comfort and confidence for both mother and infant, and induces a sense of individual agency (Keller, 2007).

Affective mother–infant FF were previously considered uniquely human (Tronick, 1989), although mutual gaze (eye-to-eye contact) occurs in agonistic interactions for NHP (e.g., Kaplan & Rogers, 2002). However, in the last 50 years, some studies have reported mother–infant FF in species of nonhuman primates (NHPs) in captivity and in semi-free ranging groups. To date, there are systematic reports regarding mother–infant FF interactions in a few species of catarrhine primates—chimpanzees (*Pan troglodytes*: Bard et al., 2005; Okamoto-Barth, Tanaka, Kawai, & Tomonaga, 2007); Japanese macaques (*Macaca fuscata*: Ehardt & Blount, 1984); rhesus monkeys (*Macaca mulatta*: Dettmer, Kaburu, Byers, et al., 2016a; Dettmer, Kaburu, Simpson, et al., 2016b; Ferrari, Paukner, Ionica, & Suomi, 2009); and pig-tailed macaques (*Macaca nemestrina*: Jensen & Gordon, 1970; Maestripieri, 1996) –, and for one platyrrhini species—squirrel monkeys (*Saimiri* sp.: Biben, 1994).

Despite differences in aims and methodological approaches, most of these studies showed that FF correlated to contact and proximity between mother and infant, during or following physical separation. These similar findings suggest that FF is a mechanism to mediate separation and to regulate proximity between mother and infant, both as a compensatory role for lack of contact during daily activities (Ehardt & Blount, 1984; Maestripieri, 1996; Okamoto-Barth et al., 2007), and as a way to resume physical contact after separation (Jensen & Gordon, 1970; Maestripieri, 1996).

Other findings for rhesus monkey indicate that FF promotes the opportunity for early emotional communication between mother and infant, driving the infants' emotional development (Ferrari et al., 2009), and contributing to the acquisition of social skills (Dettmer, Kaburu, Simpson, et al., 2016b). In the former study, there was no evidence for a role of FF (lip-smacking) in reestablishing contact or maintaining proximity between mother and infant, whereas in the latter, FF varied negatively with daily contact between mother–infant dyads.

The current research suggests that the role of mother–infant FF is similar in humans and in NHPs. However, virtually nothing is known about FF; neither for Neotropical species nor in wild populations living under relevant socioecological contexts. Most recently, we reported mother–infant FF for a wild population of capuchin monkeys (*Sapajus libidinosus*: Verderane & Izar, 2014), but we did not test the role or the stability of these interactions during early infancy. The aim of the present study is to extend the investigation of mother–infant FF in wild capuchin monkeys. Specifically, we characterized the pattern of FF between mothers and female infants in terms of frequency, context of occurrence, and consequence for proximity between the dyads across the infants' first year of life, aiming at testing the hypothesis that FF mediate physical contact between mothers and infants.

Due the importance of facial displays for communication (e.g., Carosi & Visalberghi, 2002; De Marco & Visalberghi, 2007), capuchin monkeys can be good models for investigating patterns and function of mother–infant FF early in life. Besides, as humans and

pongids, capuchins have an extensive and intimate maternal care, both in captivity (Fragaszy, Baer, & Adams-Curtis, 1991) and in semi free ranging groups (Verderane, 2005), as well as in wild populations (Verderane & Izar, 2014, 2019). The infancy is prolonged until the second year of life and in the first year, the physical contact and proximity between mother and infants decrease gradually, as well as nursing and transportation (Verderane & Izar, 2019). If FF regulate the physical contact between mothers and female infants of capuchin monkeys, we first expected that frequency of FF would (a) increase with infants' age (due to a decrease in physical contact); and/or (b) in the absence of physical contact between the dyad throughout the first year of life. In addition, if FF function as a compensatory role for lack of contact between mother and female infants (Ehardt & Blount, 1984; Maestripieri, 1996; Okamoto-Barth et al., 2007), we expected that most FF episodes would be followed by maintenance or increase in the distance between the dyad. If FF act to resume the contact after separation, then we expected that most FF episodes would be followed by the reestablishment of physical contact between the dyad.

2 | METHODS

2.1 | Study area and subjects

This study was conducted at Fazenda Boa Vista (FBV), a flat open woodland area located in the northeastern Brazilian state of Piauí (9° 39'S, 45° 25'W), within a transition zone between Cerrado and Caatinga biomes. Vegetation in FBV is mostly composed by small (3–5 m tall) xeromorphic and scleromorphic trees, forming a mosaic of physiognomies that resembling the African savannahs (for details see Presotto et al., 2018). These environmental features provide excellent conditions to follow and observe the monkeys.

The subjects were eight capuchin monkey mother–infant dyads (eight infants from 5 mothers) from one multi-male/multi-female social group (varied from 27 to 26 individuals). All infants were females and reared by their multiparous biological mothers (with one exception, a primiparous female). Since all female infants were born during data collection in the field, their ages were precisely known (Table 1). We did not include in this study four male infants that were born in the same period to avoid possible confounding effects of infants' sex (males) and mothers' parity (two males were born from primiparous mothers) on FF engagement, and because two out of them could not be followed in the first developmental points. This population has been systematically studied since 2006 by the *EthoCebus* Research Project, thus the group has been well characterized (Spagnoletti et al., 2012; Verderane, Izar, Visalberghi, & Fragaszy, 2013) and all subjects were individually recognized and habituated to human presence.

We analyzed videos of the eight subjects in the following developmental points: the first, second, third, sixth, ninth, and twelfth months of the infants' life. These developmental points comprise their first year of life, when capuchin infants gradually decrease the

TABLE 1 General information and total hours of sampling for the eight mother-female infant dyads per month of life

Dyad	Mother's parity	Infant's birth	1st	2nd	3rd	6th	9th	12th	Total per dyad
Chuchu-Cenoura	Multiparous	12/19/2013	04:04:00	09:14:50	06:55:30	01:46:29	03:19:39	02:14:41	27:35:09
Dita-Divina	Multiparous	11/07/2012	06:42:25	04:52:56	02:29:30	00:56:22	03:10:57	01:46:46	19:58:56
Doree-Donzela	Primiparous	01/14/2013 and 01/16/2013*	03:00:53	03:12:39	02:54:59	04:06:25	02:42:40	01:35:05	17:32:41
Dita-Duca	Multiparous	10/29/2014	02:31:30	03:47:16	02:41:09	02:52:23	02:33:35	01:35:16	16:01:09
Doree-Olivia	Multiparous	01/23/2015 and 01/25/2015*	02:16:01	00:39:33	00:57:25	02:59:32	01:16:04	02:30:25	10:39:00
Piaçava-Patricia	Multiparous	01/11/2013	02:08:19	02:03:34	01:38:46	02:38:12	02:11:20	01:36:23	12:16:34
Teninha-Titia	Multiparous	12/31/2012 and 01/03/2013*	02:30:43	03:22:21	02:48:57	02:43:26	02:42:21	01:49:41	15:57:29
Piaçava-Peteca	Multiparous	1/21/2014 and 11/23/2014*	02:07:15	03:49:36	01:36:02	00:01:46	04:12:18	03:22:49	15:09:46
Total per month			25:21:06	31:02:45	22:02:18	18:04:35	22:08:54	16:31:06	135:10:44

*Birth date estimated within 4-days at most (maximum interval between the last day mothers were seen after parturitions and the first time of newborns), based on their physical and behavioral characteristics when they were first seen (e.g., presence of umbilical cord, body size, and general level of activity).

dependence on their mothers for nutrition, locomotion, and protection (Fragaszy et al., 1991; Fragaszy, Visalberghi, & Fedigan, 2004; Verderane, 2005; Verderane, Izar, Verderane & Izar, 2019in press.), allowing to investigate whether FF interactions play a role in mother-infant contact and proximity. During the first three developmental points, infants are completely dependent on their mothers for nurse and locomotion, but the first contact breaks usually occur during this period (Verderane, 2005). As early as the sixth month, capuchin infants already spend a great amount of time apart from their mothers and tend to be responsible for maintaining contact between the dyad (Verderane, 2005; Verderane & Izar, 2019). At the 12th month, infants are still transported and nursed, but they spend more time apart from their mothers than in contact (Byrne & Suomi, 1995; MacKinnon, 2013; Verderane & Izar, 2019). Weaning ages in *Sapajus* spp. occur at 15.5 months for nursing and at 12.7 months for carrying (Verderane & Izar, 2019). Indeed, all female infants from our sample were still nursed and carried by their mother at the end of the 12th months.

2.2 | Data collection, processing, and coding

Videos were recorded from November 2012 to December 2015 by three observers (MJFO; MFO, AO) previously trained by MPV to videotape (with a digital hand camera) all kinds of mother-infant social interactions in the field. Observations took place five days a week, from dawn to dusk. Every week, two focal infants, chosen on a predetermined order basis, were observed per day, one in the morning and another in the afternoon, until all infants have been observed. Thus, most infants were observed for a period corresponding to a complete day per week, for four weeks per developmental point (Table 1). During these focal follows, naturalistic observations of all visible episodes of mother-infant interactions were videotaped from the beginning to the end for further identification of FF. The amount of video records obtained varied per dyad and per developmental point, totaling between ca. 10 to 27 hr per dyad and between ca. 16 to 31 hr per developmental point (Table 1).

All video recordings of mother-infant interactions were coded at Department of Experimental Psychology of the University of São Paulo by a master thesis student (R.M.A.) trained until more than 70% of intra-observer reliability in *Cohen Kappa index* for the protocol. Encodes were made with the video analysis module of Observer XT 13.0 and a total of 610 videos of mother-infant interactions were codified, from which all FF episodes were identified. Microanalyses of every episode of FF were conducted for each dyad to determine the monthly proportion of (1) interaction time spent in FF and of (2) FF episodes according to (2a) context of occurrence, (2b) immediately consequence for mother-infant contact/proximity, and (2c) the initiator of a FF. All visible episodes of FF interactions were recorded and coded from the beginning to the end. A 5 s minimum latency was established between FF episodes, with no minimum or maximum duration limit.

Based on available literature for humans and NHPs, we considered a mother-infant FF episode only reciprocal interactions,

started only if both the mother and infant had their eyes open (c.f. Ferrari et al., 2009) and their faces were oriented toward each other. Time spent in FF was recorded in seconds and according to the following categories: (a) mutual gaze: reciprocated eye to eye contact between mother and infant in the absence of other behaviors (c.f. Ferrari et al., 2009); (b) face-to-face grooming: physical contact between mother and infant faces without lip-smacking (c.f. Biben, 1994); and (c) lip-smacking: repeated lip pouting with rapid lip movement, while facing the partner (c.f. Ferrari et al., 2009) (for illustration of FF categories see supplemental movies S1 and S2).

To investigate if FF was related to lack of contact between mother and female infant, the context of each episode was classified as (a) in contact: when mother and infant bodies were in physical contact, or (b) apart: when mother and infant bodies were not in physical contact. To access if FF was related to regulation of mother-infant proximity, episodes were classified according to the immediately consequence (i.e., response of mother or infant within 20 s after a FF episode) for the spatial association as (a) retaining contact: mother and infant were in contact during FF and remained in contact after it; (b) resuming contact: mother and infant were apart during FF and resumed contact after it; or (c) retaining/increasing distance: mother and infant were apart during FF and remained or increased distance from each other after it. We also coded whether the mother or the infant was the initiator of a FF interaction (i.e., the one that first directed the face toward the other as described above). In video recordings, we used long distance focus so that the visual field was small and maximum distance between mother and infant even when apart was *ca.* one meter.

To verify the adequacy and validity of FF episodes previously encoded by R.M.A., a random sample of 140 videos (from which RMA had previously identified FF episodes in 77) were independently watched and coded by one additional judge. Coding by the two independent judges was reliable for the three categories of FF (Kappa reliability test for FF categories: mutual gaze = 0.95; face-to-face grooming = 1.00; lip-smacking = 1.00; context of occurrence = 1.00; interaction initiator = 1.00; immediately consequence = 1.00).

2.3 | Statistical procedures

Statistical analyses were conducted with IBM SPSS Statistics 24 for Windows and significance was set at $\alpha = 0.05$. Kolmogorov–Smirnov test

was used to examine the distribution of the dependent variables. For the dependent variables number of FF by context, consequence, and initiator of FF interactions, data were transformed in monthly percentage per dyads to circumvent the bias in time sampling among developmental points and dyads, and then converted into z-score to match a normal distribution.

One-way ANOVA with repeated measures was used to test whether the proportion of interaction time spent in FF (mother–infant monthly time spent in FF divided by time of interactions per dyad) increased with infants' age across the six developmental points. Two-way ANOVA with repeated measures was used to test whether the proportion of interaction time spent in FF varied by categories and infants' ages. One sample T-test and available information from the literature were used to verify if the average duration of mother–female infant FF in this capuchin monkey population differed from the average duration of FF reported for humans and squirrel monkeys.

Two-way ANOVA with repeated measures was used to test if frequency of FF episodes (monthly proportion of episodes per dyad in percentage) differed by (a) context of occurrence (presence vs. absence of physical contact between mother and female infant), (b) consequence for mother–infant contact and proximity (retain contact, resume contact vs. retain/increase distance), and (c) dyad member who initiated the interaction (mother vs. infant), and by interaction between these variables and infant' age across the six developmental points.

3 | RESULTS

3.1 | General and temporal patterns of mother–infant FF

Mother–female infant FF occurred in a rate of 9.6 episodes per hour of interaction during the infants' first year of life. FF lasted in mean (\pm SD) 6.0 ± 6.5 s, ranging from 1 to 29 s. There was a huge interindividual monthly variation (Table 2), so that the proportion of interaction time spent in FF (monthly time spent by mother–infant in FF divided by time of interactions per dyad) did not vary significantly along the first year of life of female infants (Table 3a).

Most FF episodes were mutual gaze (68%; $N = 66$), followed by facial grooming (26%; $N = 25$) and lip-smacking at face (6%; $N = 6$). The proportion of interaction time spent in FF did not significantly differ

TABLE 2 Monthly proportion of interaction time (time of FF divided by time of mother–female infant interactions) between mothers and female infants spent in FF and number of episodes across six developmental points in the first year of life

Dyad ID (M-I)	1st	2nd	3rd	6th	9th	12th
Chuchu-Cenoura	0.002 (1)	0.036 (13)	0.010 (3)	0.000 (0)	0.000 (0)	0.000 (0)
Dita-Divina	0.020 (7)	0.013 (3)	0.002 (1)	0.044 (2)	0.011 (2)	0.012 (4)
Dita-Duca	0.006 (1)	0.005 (1)	0.073 (5)	0.000 (0)	0.029 (4)	0.000 (0)
Doree-Donzela	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.043 (6)	0.000 (0)
Doree-Olivia	0.000 (0)	0.000 (0)	0.042 (2)	0.073 (4)	0.113 (1)	0.000 (0)
Piaçava-Patricia	0.000 (0)	0.025 (1)	0.031 (2)	0.010 (1)	0.006 (5)	0.017 (8)
Patricia-Peteca	0.000 (0)	0.072 (5)	0.061 (1)	0.245 (1)	0.032 (2)	0.035 (7)
Teninha-Titia	0.000 (0)	0.000 (0)	0.041 (1)	0.001 (2)	0.000 (0)	0.002 (1)

TABLE 3 Summary of statistical results for ANOVAs models

Test	Model	F	P
(a) One-way ANOVA	Time in FF X Infant age	1.491	.259
(b) Two-way ANOVA	Time in kinds of FF	2.948	.225
	Infant age	1.468	.123
	Time in kinds of FF X Infant age	1.509	.177
(c) Two-way ANOVA	Context of FF episodes	11.951	.011
	Infant age	1.235	.314
	Context of FF episodes X Infant age	0.480	.789
(d) Two-way ANOVA	Consequence of FF episodes	12.844	.006
	Infant age	1.235	.314
	Consequence of FF episodes X Infant age	0.773	.654
(e) Two-way ANOVA	Initiator of FF episodes	49.818	.001
	Infant age	1.235	.314
	Initiator of FF episodes X Infant age	0.227	.948

by FF category or by interaction between FF category and infant age (Table 3b). Qualitatively, mothers and female infants spent more time in mutual gaze than in facial grooming and in lip-smacking in most months, except in the 9th and the 12th, when they spent more time in facial grooming. Moreover, mothers and female infants spent more time in facial grooming than in lip-smacking, except in the 2nd month (Figure 1).

3.2 | Context, initiation, and consequence of mother–infant FF

Frequency of FF episodes (monthly percentage of episodes per dyad) was affected by context ($F = 11.951$; $p < .01$), occurring significantly

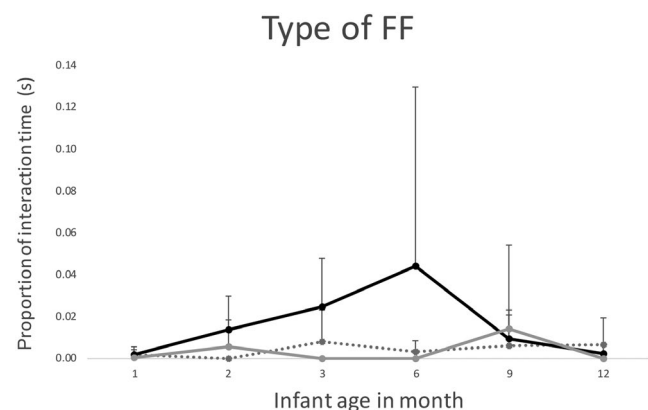


FIGURE 1 Mean monthly proportion (and standard deviation) of interaction time (time of FF divided by time of mother–female infant interactions) between mothers and female infants spent in mutual gaze (black line), facial grooming (dotted grey line), and lip-smacking (gray line) across six developmental points in the first year of life

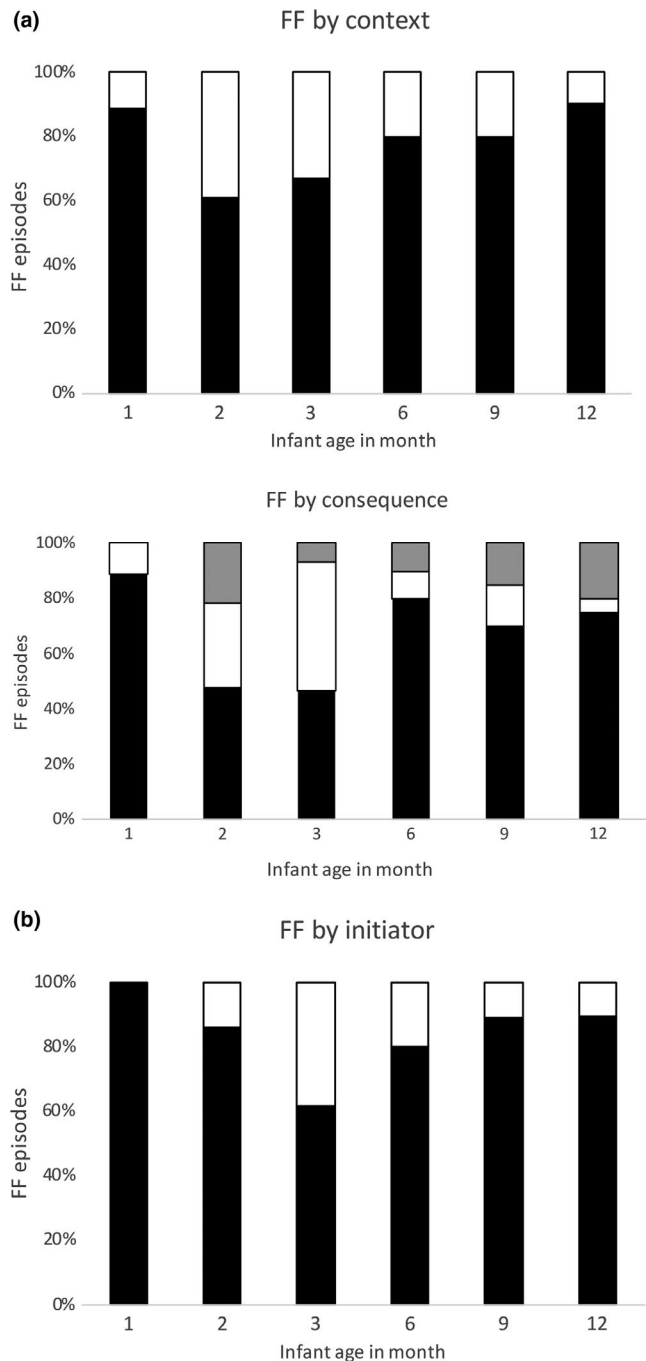


FIGURE 2 Monthly percentage of FF episodes between mothers and female infants by context of occurrence, initiator, and immediately consequence for the dyad proximity and contact six developmental points in the first year of life. (a) Monthly percentage of FF episodes between mothers and female infants during physical contact (black bars) and at distance (white bars). (b) Monthly percentage of FF episodes between mothers and female infants followed by retain contact (black bars), resume contact (white bars), and retain/increase of distance between them (gray bars). (c) monthly percentage of FF episodes between mothers and female infants initiated by mothers (black bars) and by infants (white bars)

more when mother and female infants were in physical contact (76.5%; $N = 74$) than when they were apart (23.5%; $N = 23$; Figure 2a), and by consequence for mother–infant proximity ($F = 12.844$; $p < .001$), being

followed significantly more often by maintenance of physical contact (65%; $N = 63$) than by increase/maintenance of distance between them (14.5%; $N = 14$; $p < .01$; Figure 2b). There was no significant difference in the frequency of FF followed by resume of contact (20.5%; $N = 20$) and by increase/maintenance of distance between mothers and female infants. Frequency of FF episodes was neither affected by interaction between context and infant age nor between consequence for mother-infant proximity and infant age (Table 3c and d).

Finally, frequency of FF episodes was affected by who initiated the interaction ($F = 49.818$; $p < .001$), so that mothers initiated significantly more FF (85.5%; $N = 77$) than female infants (14.5%; $N = 13$; Figure 2c), and there was no interaction between FF initiator and infant age (Table 3e). In seven episodes, we could not identify who initiated the interaction.

Most FF episodes (97%; $N = 94$) can be classified as affiliative interactions (i.e., no apparent conflict or rejection). From episodes where physical contact was resumed after the FF, 75% ($N = 15$) also resulted in mother-female infant affiliative interaction/care, namely carrying ($N = 8$), nursing ($N = 6$), and grooming ($N = 1$). Only three episodes of FF were followed by agonistic interactions between mother and infant, all of them for the same dyad (Chuchu/Cenoura) in the 2nd month of life. In the first episode, when Cenoura was seven weeks old, after she finished nursing, she moved to the mother's back, Chuchu, who immediately tried unsuccessfully to take her out by holding Cenoura with her hands, but with no FF. Then, Chuchu turned her head to Cenoura, looked her in the eyes and successfully removed her from her back. The other two episodes occurred when Cenoura was eight weeks old. When the video started Cenoura and Chuchu were already interacting, Chuchu was biting her baby softly. Then Chuchu looked her in the eyes and then slightly bite/pushed her; these was repeated two times (more than 5 s apart). In both cases, the mother initiated the FF preceding a mild rejection.

4 | DISCUSSION

This study investigated the role of face-to-face interactions (FF) between mother and their female infants in a wild population of capuchin monkeys (*Sapajus libidinosus*) to test if FF mediate physical separation and/or contact resumption between mother and infant, as reported for some captive and semi-free ranging species of non-human primates (e.g., *Pan troglodytes*: Okamoto-Barth et al., 2007; *Macaca fuscata*: Ehardt & Blount, 1984; *Macaca mulatta*: Dettmer, Kaburu, Simpson, et al., 2016b a and b; *Macaca nemestrina*: Maestripietri, 1996; *Saimiri* sp.: Biben, 1994) and humans (e.g., Keller, 2007). The long-term research on this wild capuchin monkey population afforded the opportunity to investigate this hypothesis in a naturalistic context, without the possible confounding influence of captive environments such as the attentional leaning (and FF) due to interactions with human treaters (as reported for chimpanzees by Bard, Platzman, Lester, & Suomi, 1992 and Bard et al., 2005).

We found supportive evidence for multiple functions of FF. Contrary to the initial predictions, the time spent by mothers and female infants in FF did not vary significantly across the infants' first year of life, neither did the frequency of FF episodes according to context or consequence for mother-female infant proximity. The stability and constancy of FF suggest relevance of these interactions not only early or late in infancy, but along the entire first year of female infant's life. This result might be related to capuchin monkeys' life history, characterized by an extended period of infant dependency in comparison to other haplorhines except for apes (Fragaszy et al., 2004). In this period, the infant is still dependent from the mother for nursing and carrying (Fragaszy et al., 1991; Verderane, 2005) and spend around 60% of the time in proximity with her (in less than 10m – Verderane & Izar, 2019). Further longitudinal studies assessing later life stages of infant capuchins might help to elucidate whether FF varies with age as seen in other NHP or is particularly important to this primate.

Moreover, in contrast with our predictions, FF occurred significantly more when mother and infant were in physical contact and was followed significantly more often by maintenance of physical contact. Together, these results suggest that for the mothers and female infant capuchin monkeys of this study, FF act primarily promoting opportunities for affective communication (rhesus monkeys: Ferrari et al., 2009) and intuitive care (chimpanzees: Bard et al., 2005), and perhaps would be a means for earning social skills (Dettmer, Kaburu, Simpson, et al., 2016b). Affective communication between mother and infant is not uniquely human and has been reported in chimpanzees (Bard et al., 2005) and macaques (rhesus monkeys: Ferrari et al., 2009) as a key behavior to the capacity of complex social exchanges with others. Particularly, the occurrence of FF during the first two months of life of capuchin female infants, when they spend most of their time in contact with their mothers (Verderane & Izar, 2019; Verderane unpublished data), indicates that FF also may act on mutual recognition (cf., Bard, 1994). We invite further studies with capuchin monkeys and including male infants to further explore the role of FF in a clade that presents several adaptive convergences with humans and apes (Perry, 2011).

In addition, FF were predominantly affiliative and occurred mostly as mutual gaze between mothers and female infants, not accomplished by tactile stimulation or vocalization. In a third of FF episodes mothers groomed and lip-smacked at the infants' faces, resembling the human most particular pattern of mother-infant FF communication, with specific modes of vocalizations, exaggerated mother facial expressions and kissing (Keller, 2007; Tronick, 1989), and in chimpanzees (Bard et al., 2005) and macaques (Ferrari et al., 2009; Maestripietri, 1996). Although there was no statistical difference, qualitatively mothers and female infants spent relatively more time in mutual gaze and the lip-smacking than in facial grooming from the first to the sixth months of life, but the pattern was opposite in the ninth and twelfth months. This result resembles the interchangeability between tactile and visual modes of mother-infant affective interaction reported for humans (Keller, 2007) and chimpanzees

(Bard et al., 2005), but further studies with the appropriate design are necessary to directly test this hypothesis in capuchins.

We found that FF play a role in resuming physical contact between mother and female infant in wild capuchin monkeys. A quarter of FF occurred in the absence of physical contact between the dyad and in most of them, physical contact was resumed following the FF. The contact resumed after the FF was often accompanied by intimate affiliative interactions and maternal care, which supports the hypothesis that FF mediates affective communication (Ferrari et al., 2009) and intuitive care (Bard et al., 2005).

Capuchin mothers were the main responsible for initiating FF along the first year of infants' life, but female infants also actively assumed this role from the second month of life onwards. FF represented a small proportion of mother–infant interactions, but the average duration of FF bouts observed here did not differ from that reported for humans (Bard et al., 2005) and was slightly longer than that reported for squirrel monkeys (Biben, 1994). Moreover, about 40% of FF episodes lasted longer than 6s, whereas it seems that chimpanzees had bouts no longer than 6s (Bard et al., 2005). The mean duration of mother–female infant FF observed in this capuchin population did not differ from that reported for humans (reference value = 6.0 s; Bard et al., 2005) and tended to be longer than mean duration reported for captive squirrel monkeys ($t_{97} = 1.9$; $p = .06$; reference value = 4.6 s; Biben, 1994). Taken together, these results suggest that mother–infant FF are biologically relevant for bearded capuchin monkeys, at least for female infants, as is the case for humans (e.g., Lavelli & Fogel, 2002) and other more distant related NHPs, for which data are available (Bard et al., 2005; Biben, 1994; Dettmer, Kaburu, Simpson, et al., 2016b; Ferrari et al., 2009; Jensen & Gordon, 1970; Maestripieri, 1996; Okamoto-Barth et al., 2007). This adds external validity for hypotheses of a general function of FF with the Primate order.

Since only FF interactions between mothers and female infants were investigated here, we cannot exclude the possibility that results with infant males would be different. Female bearded capuchin monkeys are phylopatric and males usually disperse slightly before achieving sexual maturity (Fragaszy et al., 2016; Verderane et al., 2013). Primate maternal investment might be affected by the possible reproductive future of their offspring (Silk, Clark-Wheatley, Rodman, & Samuels, 1981), which is often dependent on dispersal (Pope, 2000). In captive rhesus macaques, FF is more frequent between mother and male infants (Dettmer, Kaburu, Byers, et al., 2016a), and these differences are related to future differences in social capacities of the offspring (Dettmer, Kaburu, Simpson, et al., 2016b). The evidence so far on differences in maternal investment according to the sex of offspring comes primarily from research on cercopithecines (Lonsdorf, 2017), so that future comprehensive research on wild capuchin monkeys and from a wide range of primate species will help to elucidate these questions.

To our knowledge, this is the first systematic study reporting the occurrence, pattern, and evidence for the function of mother–infant FF for a wild Platyrrhini, adding evidence and external validity of mother–infant FF interactions. We believe this is the first step

toward further investigations on the relation of FF and socioecological variables across populations of capuchin monkeys and other primate species.

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DATA AVAILABILITY STATEMENT

The authors state that data that support the findings of this study are available from the corresponding author upon reasonable request.

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