

Article

Maternal care styles in primates: considering a New World species¹

Michele P. Verderane* Patrícia Izar 

University of São Paulo, Institute of Psychology, São Paulo, SP, Brazil

Abstract: When aiming understand the human behavior, comparisons with nonhuman primates are especially relevant to identify homoplasies (similar characteristics that evolve independently in different species). In this paper, we present a two-year longitudinal study on the maternal behavior of capuchin monkeys (*Sapajus* spp.) under naturalistic conditions. Our results reveal distinct maternal care styles within a continuum ranging from permissiveness (*laissez-faire*) to protectiveness. The observed development of mothers and infants bond suggests that the dependence period of capuchin monkeys infants involves, in addition to physical maturation processes, the establishment and development of psychological processes associated with the attachment system. It is possible that the variability of maternal styles – resulting from the combination of mothers' and infants' characteristics, as well as socioecological contexts, along with the extension of the attachment bond – are responsible for paving the way for different developmental trajectories. This may be one of the mechanisms underlying interindividual differences arise in adult populations, as seen in humans.

Keywords: attachment, mother-infant interaction, parenting care, infancy, *Sapajus*.

Introduction

The idea that women have an unconditional natural predisposition to cling to and care for a baby, often referred to as maternal instinct, is called into question by cases of maternal abandonment and even neonaticide. Both have been recorded throughout history and in different cultures (Badinter, 1985). For Sarah Hrdy (1999), these extreme cases reveal that women's predisposition to maternal care varies according to contingencies associated with their livelihoods, their children's needs, and their own reproductive future. In modern life, in addition to economic and social-support conditions, these contingencies include cultural expectations, sexual roles, honor and shame, sexual preferences and expectations for the future. Hrdy's thesis was developed from an ethological perspective, characterized by comparative analysis of human and nonhuman animals. Its goal was to understand the internal regulatory mechanisms of specific behaviors, the stimuli that elicits them, and their changes throughout development, as well as their evolutionary history and survival value (Tinbergen, 1963). Comparative analysis allows for the identification of characteristics of a species that are shared by other, closely related species. This suggests either a common ancestry (i.e., a homology)

or that these characteristics are exclusive. When homoplasies are identified – that is, when functionally alike (physiological, morphological, psychological) characteristics evolve independently in different species, under the same selective pressures and serve to the same function – adaptation can be inferred.

Due to sexual differences in reproductive physiology (gamete production, fertilization, and internal gestation), females are more predisposed than males to invest in parental care. Thus, in this article we will approach exclusively the maternal parental care. From an ethological perspective, maternal care has evolved due to increasing infants' chances of survival, at the expense of a diminishing in mothers' ability to invest in additional offspring (Trivers, 1972). From the standpoint of individual fitness (i.e., reproductive success), this condition rises an "evolutionary conflict." For mothers, it is more advantageous to stop care for their current infants as soon as they are able to survive on their own. For infants, it is more advantageous to keep receiving care as long as possible. Evolutionary theory predicts that when the costs of offspring care outweigh its benefits, selection favors maternal rejection behaviors (Trivers, 1974). Advantages obtained from mothers' refusal of care will depend on their infants' ability to survive independently.

For effective maternal care, physical proximity between mothers and infants is essential. Attachment Theory (Ainsworth, 1979; Bowlby, 1969) proposes that mother-infant bonding is an adaptive feature of many animal species, including humans. Such

* Corresponding address: miverderane@gmail.com

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bonding was shaped by natural selection due to promoting the protection of immature offspring. The attachment system is a set of behaviors that promote the formation and maintenance of the proximity bond and the socio-affective interaction between mother and infant. This system is essential for the child's development and forms the basis for future social relationships and personality development. Its primary function is to ensure proximity between the infant and its primary caregiver (the mother in the case of mammals), ensuring the protection and comfort essential for their physical development (Ainsworth & Bowlby, 1991).

In this scenario, the transition between dependence on maternal care for survival and self-sufficient life is often marked by conflicts between mothers and offspring (Altmann, 1980; Trivers, 1974). In primates, infancy is defined as the period in which the infant is physically depends on the mother to survival. The most commonly used point of reference for determining the end of such a period is the age of nutritional and locomotor weaning (i.e., when the infant is no longer fed on the mother's milk and is no longer carried by the mother) (Lonsdorf, 2017; Pereira & Altmann, 1985). However, within each species' range of behavioral flexibility, the timing and strength of maternal rejection can be quite variable, suggesting that other processes participate in this dynamic (Verderane, 2005). According to Ethology, maternal behavior's final expression is a combination of the species' repertoire, the individual characteristics of mothers and infants, and the socioecological environment in which they live (Altmann, 1980).

Nonhuman primates are especially interesting for ethological, comparative studies of the mother-infant relationship. Their occurrence in a wide variety of environments allows for the investigation of complex hypotheses on the causes of behavioral flexibility. Moreover, because of their common ancestry to humans – with whom they share a number of homologous characteristics – nonhuman primates offer a window into the evolutionary basis of human behavior.

Except for a few species with biparental care – which is particularly common in the Callitrichidae family (Yamamoto et al., 2014) – maternal parental care prevails among more than 300 nonhuman primate species (Maestriperi, 2001). In this way, mothers are primarily responsible for nursing, carrying and protecting infants, as well as helping them to deal with their physical and social environment (Berman, 1980; Verderane, 2005). Therefore, during infancy – which is particularly long in the primate order – the mother represents the infant's strongest social bond. This prolonged maternal bond is not only fundamental to effective maternal care but can also contribute to infants' learning process. For example, the

mother can be a model for the acquisition of foraging techniques (Maestriperi, Ross, & Megna, 2002), or as a secure base in situations where the infant faces new challenges (Okamoto-Barth, Tanaka, Kawai, & Tomonaga, 2007). The way mothers take care of their infants' needs, however, is variable. These variations amount to distinct maternal care styles.

According to the literature, which is based exclusively on the study of Old World species², maternal care style emerges from the combination of rejection and protection behaviors (Altmann, 1980). There are two classification models for nonhuman primates' maternal care styles. According to Altmann, the traditional model classifies mothers as restrictive or *laissez-faire*. Restrictive mothers nurse, carry, groom their infants, maintaining greater spatial proximity to them; while *laissez-faire* mothers exhibit the opposite pattern (Altmann, 1980). In a different classificatory scheme, Maestriperi (1999) argues that the combination of the two components of maternal care, protectiveness and rejection, generates four possible maternal styles; (1) protective: high in protectiveness and low in rejection; (2) controlling: high in both protectiveness and rejection; (3) rejecting: low in protectiveness and high in rejection; (4) *laissez-faire*; low in both protectiveness and rejection.

As in humans (Carvalho, Seidl-de-Moura, Martins, & Vieira, 2014), nonhuman primates' differences in maternal care style – either among populations of the same species or among individuals of the same population or social group – stem from individual characteristics of mothers (e.g., reproductive experience, rank in the dominance hierarchy, temperament) and infants (e.g., sex, temperament), as well as from the dyad's interaction with their socioecological environment (e.g., risks of death for mother and infant, food supply patterns, social group size and composition) (Dettmer et al., 2016; Fairbanks, 2003; Li, Ren, Li, Zhu, & Li, 2013; Saltzman, & Maestriperi, 2011). For example, mothers who perceive their infants are under high risk – such as subordinate and primiparous females – and mothers in despotic societies generally exhibit a more protective style than their counterparts in less-dangerous contexts (Li et al., 2013; Verderane & Izar, 2014). In *rhesus* macaque (*Macaca mulatta*), mothers who raise their infants in the presence of the family have a *laissez-faire* care style, while mothers with few or no relatives in the social group tend to be protective (Berman, Rasmussen, & Stephen, 1997). In several species of cercopithecoids (an Old World primate group), mothers living in unpredictable environments are less responsive to the needs of their infants, especially if

2 Old World primates belong to the Catarrhini suborder. This suborder's divergence from New World species (which belong to the Platyrrhini suborder) occurred at least 40 million years ago (Chatterjee, Ho, Barnes, & Groves, 2009).

the demands for survival are high and the food supply irregular (Rosenblum & Andrews, 1994).

Paradoxically, despite the great progress achieved during recent decades in the understanding of maternal care style and its variables, the literature still has gaps stemming from its reliance on a limited number of Old World species and on the study of captive groups and populations. When aiming to understand human behavior, the study of New World primates is especially relevant for identifying homoplasies. Thus, this paper presents the results of a two-year study on the maternal behavior of capuchin monkeys (genus *Sapajus*) under naturalistic conditions. Our observations allowed us to identify distinct maternal styles within a continuum ranging from permissiveness (*laissez-faire*) to protectiveness. We were also able to identify the development pattern of the attachment bond between mothers and infants. The capuchin monkey is a Neotropical primate that exhibits great behavioral flexibility due to its wide range of habitats inhabited and expansive geographical distribution. It possesses numerous adaptive convergences with pongids and humans, including prolonged infancy and immaturity of the infant at birth (Fragaszy, Visalberghi, & Fedigan, 2004).³ These characteristics make capuchin monkeys ideal models for this research proposal. Studies with species that are phylogenetically distant from those of the Old World primates and from humans can provide evidence about our psychological and behavioral adaptations, highlighting homologies regarding maternal care and mother-infant attachment.

Methods

Study site and subjects

Our study was conducted at the Tietê Ecological Park (PET – *Parque Ecológico do Tietê*), in the city of São Paulo, with a group of capuchin monkeys that inhabit a reforested area of 19.5 ha within the park's limits. The site is home to a variety of botanical and animal species, many of which are consumed by capuchin monkeys. Conversely, however, the park has no natural predators for primates. Monkeys roam freely in the area, feeding on naturally available forest resources and a mix of fruits and vegetables supplied daily by PET biologists (Verderane, 2005).

The subjects of this study were five mother-infant dyads (1 male and 4 females of 3 multiparous and 2 primiparous mothers⁴) from a group of capuchin monkeys comprised of 22 individuals (5 adult males and 5 adult females; 3 juvenile males and

2 juvenile females; 2 infant males and 5 infant females – Table 1) in an organization similar to that of wild capuchin monkeys (Izar & Ferreira, 2007). Our data are naturalistic observations of these five dyads throughout the entire period between birth and the 15th month of life. We used additional data and repeat-measure analyses to investigate whether the study's three multiparous mothers were consistent in how they nursed and carried successive infants. These analyses were performed with eight infants – five from the present study, and three from a previous one (within the same population) (Resende, 2004) – totaling four infants born from Física (Fractal, Filó, Frida and Fábio), two from Ana (Ada and Angélica) and two from Janete (Janeiro and Jujuba).

Sampling method and behavioral variables

Data were collected over 26 months, from February 2002 to April 2004, totaling 422 hours of observation of mothers and infants. Behavioral recordings were made by M.P.V. using the Focal-animal method (Altmann, 1974), with a sample interval of 10 minutes and instantaneous records every minute. The first month of study was devoted to training the researcher in regard to sampling method, behavioral categories, and calibration (to learn how to estimate the physical distances between mothers and infants). Each mother and each infant were observed at least once a week, according to an order previously determined by draw. An equitable distribution between morning (06:00–12:00) and afternoon (12:01–17:00) was respected, as well as an interval of one hour between observations of the same individual. Not more than two observations of an individual in each period were performed in the same day.

To investigate maternal care style, we used the following behavioral variables (frequency normalized by dyad observation time): (1) Nursing; (2) Maternal carrying; (3) Grooming (i.e., mother cleans the infant); (4) Food sharing (i.e., mother shares solid food with the infant); (5) Rejection (i.e., hitting or threatening the infant); (6) Maintaining physical proximity to the infant (see below).

To investigate the process of infant independence, we used the independent feeding and locomotion as behavioral variables (frequency normalized by infant observation time). The last records of nursing and maternal carrying were used to determine nutritional and locomotor weaning ages of each infant, respectively.

The development of the physical-proximity bond between mother and infant was evaluated based on two criteria. A proximity index was used to determine which member of the dyad was primarily responsible for maintaining and restoring physical proximity between the members of the dyad (Hinde & Atkinson, 1970). To assess dynamics of spatial association, we calculated the time (proportion of focal samplings) during which

3 Family of primates with whose common ancestry is the closest to humans. Includes the orangutan, the gorilla and the chimpanzee.

4 The term primiparous refers to a female whose current offspring has been the only one so far. The term multiparous refers to a female who has had more than one offspring.

mother and infant remained at distances of: (1) up to 1 meter; (2) 1.1 meters to 10 meters; (3) more than 10 meters from each other.

Results and discussion

Maternal styles in capuchin monkeys

As we stated earlier, maternal care style in nonhuman primates consists of individual differences in maternal care parameters that persist across the rearing of successive infants. Thus, we first verified whether capuchin monkey mothers in our study had distinct maternal styles. The traditional approach (maternal protection and rejection continuum) was used. Cluster analysis was employed to compare the relative (i.e., normalized by dyad observation time) frequency of six maternal behaviors: nursing (mother feed infant via breastfeeding); carrying (mother carries infant close to her body); maintenance of proximity (mother approaches or makes contact with infant); grooming (mother cleans infant's fur); solid food sharing (mother allows infant to eat the same food she eats); rejection (mother threatens or hits infant, or prevents infant from accessing the abovementioned forms of care). The mothers were grouped according to similar profiles in each of these variables. We then verified if the clusters differed significantly in terms of maternal care variables.

Is there variations in maternal care styles among the studied capuchin monkeys?

We identified three distinct maternal care styles among the five monitored females. Ana's style of care

was characterized by a higher frequency of nursing in comparison to Física's, Janete's and Cisca's, higher frequency of carrying in comparison to Física's and Janete's, and more responsibility for maintaining physical proximity to the infant in comparison to all other females. Ana's infants were also weaned later than Física's, Janete's and Cisca's. In addition to these differences in regard to Ana, Física also had a lower frequency of nursing and infant carrying. She also established the independence of infants earlier than Vavá. Moreover, Física was the mother who most frequently groomed her infant, followed by Janete, Ana, and Vavá and Cisca, who had the lowest frequencies of grooming. Inversely, Cisca was the mother with the highest infant rejection rates, followed by Janete, Ana, Vavá and Física (Table 1).

We found that the maternal style varied in a continuum of investment in nursing, carrying, and maintenance of physical proximity to the infant across the infancy. We employed the traditional classification by Altmann (1980) as a basis but, instead of the dichotomous categorization proposed by the author, we adopted a continuum ranging from maternal permissiveness to protectiveness, in which the extremes correspond to the *laissez-faire* and protective styles (Figure 1). This nomenclature was adopted because it better reflected the nature of the maternal pattern exhibited by capuchin females. Food Sharing, rejecting, and grooming the infant are also components of maternal style; but they either do not relate to permissiveness and protectiveness, or reflect characteristics of the mother's temperament, which combine flexibly with the other elements of care.

Table 1. Mean time (% of dyad observation time) devoted by capuchin mothers to care behaviors between birth and 15 months of age

Dyad	Nursing (%)	Carrying (%)	Proximity (PI) ^a	Grooming (%)	Food sharing (%)	Rejection (%)	Nutritional weaning (month)*	Locomotor weaning (month)**	Maternal care style
Ana/Angélica	7.6	43	-36	0.32	0.04	0.009	20	13	Protective
Cisca/Cláudia	6.0	34.5	17	0.17	0.04	0.03	14	14	Permissive-intermediate
Física/Frida	3.8	27.5	24	0.14	0.03	0.003	10	8	Permissive
Janete/Jujuba	5.2	28	20	0.09	0.05	0.01	*	*	Permissive-intermediate
Vavá/Vítor	7.7	41.5	22	0.2	0.12	0.008	18	16	Protective-intermediate

^aMean Proximity Index value; *Jujuba died at the 15th month of life, while she was still nursed and carried by the mother.

*Infant age at the last nursing bout

**Infant age at the last maternal carrying bout.

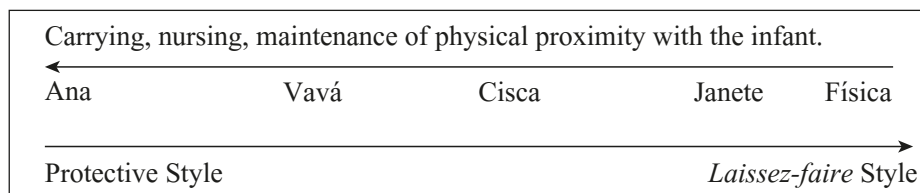


Figure 1. Classification of maternal care style of the five females within a continuum of restrictiveness and permissiveness (according to investment in breastfeeding, carrying, and maintenance of proximity to the infant).

Thus, Ana and Física had the two most distinct styles. Janete, Cisca and Vavá presented an intermediate style, that is, their maternal care style had parameters typical of both the protective and *laissez-faire* styles. According to Altmann's (1980) dichotomous classification model, Física, Janete and Cisca would have a *laissez-faire* maternal style, while Ana and Vavá would have a restrictive style. In Maestripieri's (1999) classification, Física, Janete and Cisca would be considered slightly protective, and Ana and Vavá would be considered very protective, given their investments in nursing, carrying and maintenance of physical proximity with their infants. However, due to her infant rejection rates, Física would be considered a relaxed mother (low degree of protectiveness and rejection, i.e., *laissez-faire*), Janete and Cisca would be considered rejecting mothers (low degree of protectiveness and high rejection), Ana would have a controlling style (high degree of protectiveness and rejection), and Vavá would have a protective style (high degree of protectiveness and low rejection).

At first glance, these results fit the maternal style profiles proposed by the Altmann (1980) and Maestripieri (1999) models. However, when we considered grooming and food sharing in the classification, incompatibilities emerged between the previously examined care variables and the models expectations. For both models, it would be expected that maternal grooming and food sharing would be positively correlated with the other protective variables. What we actually observed, however, were combinations that differed from these expectations.

We suggest two possible and non-exclusive explanations. The various combinations between grooming, food sharing and other variables of maternal care may indicate that these elements comprise the maternal style but do not fit within the dimensions of protection and rejection. In fact, more recent studies propose the existence of a third dimension of care in nonhuman primates, called maternal warmth (Maestripieri, Hoffman, Anderson, Carter, & Higley, 2009), regarding intimate interactions with the infant. This dimension still poorly understood. At the same time, it is possible that in capuchin monkeys (genus *Sapajus*) and perhaps in other New World primate species – as compared to Old World species, whose study underlies the classification systems currently in use – these two dimension of maternal care combines in a more flexible

manner with the other components of care. Indeed, some categories of maternal protection and rejection observed in this study were quite distinct from those often reported for Old World primates. For example, restricting the infant movement, preventing it from breaking contact or straying, or punishing its attempts to obtain care with physical aggression were absent behaviors among capuchin mothers from PET. In addition, episodes of “infant retrieval” were rare – in which the mother stops what she is doing to retrieve the infant and interrupt its activity, such as social interactions with other members of the social group.

These results show marked differences in the maternal repertoire between these two branches of the primate order. This may be the combined result of adaptations to different evolutionary pressures and flexible responses to the characteristics of the socioecological context in which mothers and infants live. The typical social structure of capuchin monkeys (genus *Sapajus*) is less risky to infants than that of Old World primates (less despotic and more egalitarian dominance relationships, lower risk of infanticide, more tolerance between females, interest and participation of multiple members of the group in infant care) (Fragaszy et al., 2004; Izar et al., 2006; Izar et al., 2012; Verderane, 2005; Verderane & Izar, 2007; Verderane, Izar, Visalberghi, & Fragaszy, 2013). Moreover, at PET the food supply is abundant and there are no capuchin's predators neither long distances to be traveled by individuals, which provide a less-risky life for infants. This combination of characteristics may be responsible for the differences in maternal repertoire reported above.

Why do capuchin monkey females differ in their maternal care styles?

As in humans, maternal style in nonhuman primates may vary depending on the socioecological environment in which mothers and infants are inserted, such as food supply and predation risk, and on the basis of the intrinsic characteristics of mothers and infants, such as social status, matrilineal size, and infant sex (Bercovitch, 2002; Fairbanks, 2003; Li et al., 2013; Maestripieri, 1999). In our research, we investigated the effects of mothers' parity (i.e., reproductive experience), dominance (i.e., individual position within the group

dominance hierarchy), and family and affiliation network over their maternal style.

Patterns of carrying and nursing by the three multiparous females (Física, Ana and Janete) were consistent across successive infants, although all of them changed position in the group dominance hierarchy (Falótico, Verderane, Resende, Ottoni, & Izar, 2003) and experienced changes in the size of their families due to deaths, births, and migrations more than once. Furthermore, Física and Ana, the two oldest females in the group, presented the most stable maternal but also the most distinct from one another. However, the two primiparous females (Vavá and Cisca) had the least consistent maternal styles, classified as protective-intermediate and permissive-intermediate, respectively. In a subsequent study with this same study group, Carminatti (2009) observed that primiparous females (N = 4) invested more in nursing, carrying and maintaining proximity to their infants than multiparous females, but the differences were not significant due to the great behavioral variability of primiparous mothers.

Thus, we suggest that maternal experience affects the stability of maternal style in capuchin monkeys, with multiparous females presenting consistent profiles over time and few permeability to social fluctuations. However, unlike Old World species, parity did not determine the specific care style adopted by each female.

Mother-infant bond in capuchin monkeys: attachment and conflict

Proximity and physical contact between mother and infant are essential to effective maternal care

$$\frac{N. \text{ of MC occurrences}}{\sum N. \text{ of MC by infants} + N. \text{ of MC by mothers}} - \frac{N. \text{ of BC occurrences}}{\sum N. \text{ of BC by infants} + N. \text{ of BC by mothers}}$$

Positive values indicate that the infant is primarily responsible for approaching and contacting the mother, while negative values indicate the opposite (Hinde & Atkinson, 1970). In addition, we analyzed the timing and context of infants nutritional and locomotor weaning and mother-infant conflicts.

Development of mother-infant bond in capuchin monkeys

Between birth and the second month of life, all infants were exclusively dependent on their mothers for nutrition and locomotion, remaining all the time in contact with them. The Proximity Index (PI) for this period was zero, since there was no contact break

and to the infant's survival, ensuring protection and comfort for a healthy physical, social, and emotional development during infancy. While the attachment mechanism ensures the proximity necessary for the mother-infant relationship develops, it also imposes for both a process of separation, resulting from the maturing of the infant's skills and weaning. We used data on spatial association, responsibility for maintaining contact, and mother-infant conflict to investigate the development of the attachment bond between capuchin monkey mothers and infants as well as the degree of dependence of the infants from their mother, from the birth to weaning.

First, we analyzed the evolution of the spatial relationship between mother and infant, comparing the monthly frequency of three categories of physical distance: (1) in contact (up to 1-meter distance); (2) from 1.1 meters to 10 meters; (3) more than 10 meters. Next, we evaluated the respective roles of mothers and infants in regard to maintaining physical proximity. This analysis was based on the behaviors of "break contact" (BC – dyad is in contact or dyad members are up to 1-meter apart from each other and mother or infant breaks contact or moves away) and "make contact" (MC – dyad members are separated and mother or infant approaches or makes contact). Subsequently, we calculated the monthly frequency in which mother and infant "make contact" and "break contact" with each other. To determine which member of the dyad was primarily responsible for maintaining proximity, we used the Proximity Index (or Hinde Index), according to the following formula:

between mothers and infants. In the third month, infants began to break contact and move away from their mothers, starting the process of independent locomotion and feeding. From then on, there was an accelerated and constant decrease in the time mothers and infants remained in contact (i.e., up to one meter apart). In the sixth month of infants' lives, contact time decreased to less than 45% of total observation time. The absence of rejections and conflicts shows that separation was at the initiative of the infants to explore their surroundings, and not due to maternal rejection. In fact, negative PI values show that mothers were primarily responsible for maintaining physical proximity to their infants as the latter began to explore the environment independently (Figure 2).

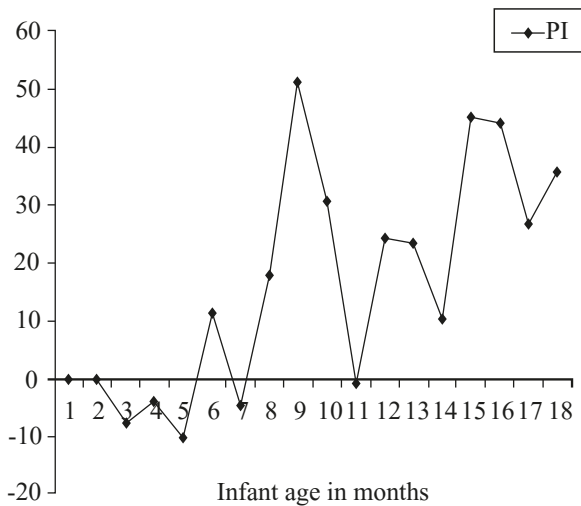


Figure 2. Distribution of Proximity Index (PI) values between mothers and infants from the first to the 18th month of infants' lives

In the eighth month, mother-infant contact (i.e., up to one-meter distance between mother and infant) time reached the lowest level throughout the infants' first year of life. From then on, the PI reversed and started to show positive values, indicating that infants assumed the responsibility for maintaining proximity to their mothers. This pattern was preserved until the end of the 18th month (except for the 7th and 11th month – Figure 2). The eighth month was also marked by the beginning of maternal rejections and the mother-infant conflicts resulting from these rejections. These indicate the beginning of the weaning process. It is noteworthy that, precisely at this stage, infants went through significant behavioral changes, devoting as much time as adults to locomotion and independent feeding. This suggests that at this point infants are already able to survive by themselves. In one case, an infant (Fábio) was able to survive after being completely weaned by his mother (Física) at the ninth month of life (Verderane & Izar, 2007). This corroborates our argument that capuchin monkeys in the PET can feed and move independently before the first year of life.

However, in the ninth month, there was an impressive infant response to maternal refusal to provide care. Independent feeding and locomotion behaviors diminished, with a corresponding increase in nursing and carrying by the mother and a return to the development pattern that had been prevalent before the eighth month. The highest peak of contacts (PI) initiated by infants during this month shows that they were primarily responsible for this situation (Figure 2).

From the first year onward, mother-infant contact time dropped and remained lower than 25% of total observation time. However, at the end of the 18th month of life, mothers and infants still spent a long time – 70% of total observation time – within a 10-meter apart from each other (Figure 3). In this phase, the weaning process accompanied by infants resistance to it remains. There were two cycles of reduced contact

time and increased distance between mothers and infants, followed by returns to previous levels (i.e., increased contact time) associated with peaks in the number of infant approaches. Subsequently, contact time was reduced to even lower values.

On average, nutritional weaning occurred at 16 months of age, and locomotor weaning at 13.5 months. Thus, we found that infants' independence – that is, the moment they completely stop being fed and carried by their mothers – occurred about a year after the weaning process began, long after they were already able to feed and locomote independently.

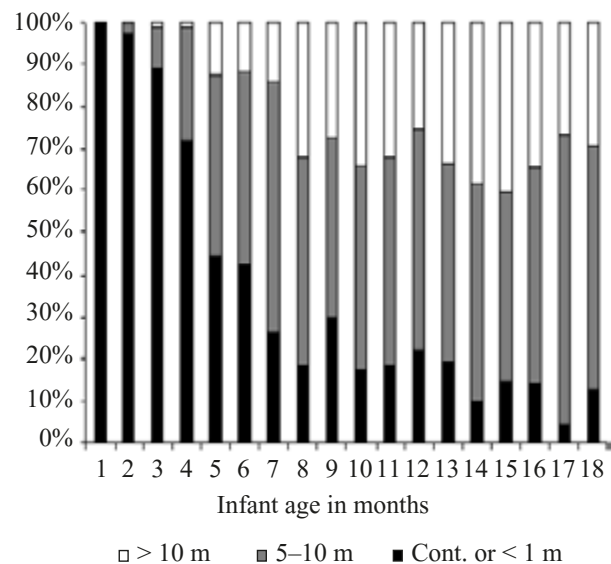


Figure 3. Distribution of distance categories among mothers and infants from first to 18th month of infants' life

If infants can survive on their own, why does weaning occur later?

Considering that, from the sixth month of life onward, infants were primarily responsible for maintaining contact with their mothers, we suggest that they had an active role in prolonging maternal care beyond their actual survival needs. Therefore, late weaning may be the result of infants' resistance against no longer being fed and carried by their mothers. But the question remains: if infants have reached a point where they could feed and locomote on their own, why do they resist no longer being nursed and carried by their mothers?

We suggest that the period of dependence of primate infants is not only related to their physical maturity, but also to psychological processes, especially the establishment and development of attachment bonds with the mother, as well as the learning of complex skills (Verderane, 2005). Prolonged immaturity is typical of primates and is related to slower development, large brains, and greater dependence on learning abilities that are typical to the species (Janson & van Schaik, 1993; Joffe, 1997). In this regard, capuchin monkeys stand

out for the immaturity of their infants at birth and for sustaining one of the longest immaturity periods among primates – approximately 13% of life between birth and sexual maturity, assuming a life expectancy of 40 years (Fragaszy & Bard, 1996). This indicates the importance of the infant's attachment bond with the mother. This adaptation would ensure the necessary conditions for learning about the species behavioral repertoire, which involves sophisticated foraging techniques such as the use of tools, as well as a complex social structure (Coelho et al., 2015; Fragaszy et al., 2013; Verderane et al., 2013; Resende, Ottoni, & Fragaszy, 2008; Verderane, 2005). This pattern is more reminiscent of pongids and humans than similarly sized species (Fragaszy, Baer, & Adams-Curtis, 1991).

The role of maternal rejection in the process of infant independence is more controversial. Some authors understand maternal rejection as a mechanism that promotes the infant independence (Schino, Speranza, & Troisi, 2001), while others argue the opposite, that maternal rejection increases the infant attachment to its mother (Bowlby, 1969). Our results partially support both hypotheses. At first, maternal rejections led infants to increase seeking for maternal care, although their locomotor and feeding skills were already well developed. Subsequently, infants seem to accommodate or “accept” the mother's rejection. Thus, rejection gradually promotes independence. However, mothers are not immune to infants resistance to their refusal to provide care. They respond to intense demands by loosening rejection and the weaning process, extending the dependence bond.

Why mothers do not reject their infants?

According to Trivers' (1972) parental investment theory, mother-offspring conflict occurs because parental care increases the chances of infant survival, at the expense of parents' reproductive ability. The conflict lies in the fact that it is more advantageous for the mother to disengage from her current infant as soon as possible and invest in raising another offspring. For the infant, it is more advantageous to extend the care period for as long as possible.

This flexibility may result from the variability of ontogenetic trajectories, affected by distinct ecological and social factors. Therefore, it is plausible that the behavioral bases of these differences manifest very early in infant development, being modulated by specific mother-infant attachment patterns and care styles resulting from distinct social and ecological pressures.

Although we would expect capuchin monkey mothers to resist infants' attempts to maintain maternal care from the moment they are able to survive on their own, the dyad relationship is a two-party social system, with a mutual regulation of the behavior and physiology of mothers and infants. Thus, although most studies on mother-infant attachment in primates focus on the importance of

attachment for infant development – for review on this subject see Rosenblum and Paullly (1991) – it is known that behavioral (or psychological) mechanisms also ensure the mother bond to the infant (Maestripieri, 2001). Our study offers an additional contribution by showing that this attachment is a dynamic process, in which mother and infant become mutually attached and perform active, distinct, and changing roles throughout infancy.

Conclusion

In this study, we report the existence of distinct maternal care styles in a New World species of nonhuman primates, the capuchin monkey. Mother-infant attachment is a dynamic process, in which mothers and infants participate in and respond to each other behaviors. It is maintained far beyond the infant survival needs. Despite the limited number of dyads observed, our findings are stimulating and allow us to propose some hypotheses that may be tested in future investigations.

It is possible that the variability of maternal styles – resulting from the combination of mothers and infants characteristics, as well as socioecological contexts, along with the extension of attachment bond – are responsible for paving the way for different developmental trajectories. This may be one of the mechanisms by which interindividual differences arise and consolidate in adult capuchin monkey populations, as observed in human populations.

The incongruities between maternal behaviors clearly associated with protection and rejection (nursing, carrying and physical proximity to the infant) and the other care variables (grooming and food sharing) suggest the existence of a third dimension of maternal style, as recently suggested in the literature. The maternal warmth dimension refers to the extent of intimate mother-infant interactions (Maestripieri, Hoffman, Anderson, Carter, & Higley, 2009), such as intimate body contact and face-to-face interactions (Byrne & Suomi, 2009). It resembles human parenting in several aspects, but is still poorly understood in nonhuman primates.

In a previous study aimed understanding maternal warmth in wild capuchin monkeys, we found that the repertoire of intimate interactions between mothers and infants is more extensive and sophisticated than previously assumed, and includes distinct forms of tactile stimulation of the infant, as well as face-to-face interactions (Verderane & Izar, 2014). The choice of a phylogenetically distant species to investigate the role of this affective interaction in the quality and extent of the mother-infant attachment bond – and in the infants' socio-emotional skills development of– uncovers traits of affection that were once considered exclusively human, opening a fascinating comparative perspective for a broader understanding of the biological basis of human parenting.

Estilos de cuidado materno em primatas: considerações a partir de uma espécie do Novo Mundo

Resumo: Quando buscamos entender o comportamento humano, comparações com primatas não humanos são especialmente relevantes para identificar homoplasias (características semelhantes que evoluem independentemente em diferentes espécies). Neste artigo, apresentamos um estudo longitudinal de dois anos sobre o comportamento materno de macacos-prego (*Sapajus* spp.) em condições naturalísticas. Nossos resultados permitiram identificar estilos de cuidado distintos dentro de um contínuo de permissividade a proteção. O desenvolvimento observado do vínculo entre mães e filhotes sugere que o período de dependência de filhotes de macaco-prego envolve, além de processos de maturação física, o estabelecimento e desenvolvimento de processos psicológicos associados ao sistema de apego. É possível que a variabilidade de estilos maternos resultante da combinação de características de mães, filhotes e contextos socioecológicos, aliada ao prolongamento do vínculo de apego, pavimente caminhos para diferentes trajetórias de desenvolvimento. Como em humanos, esse pode ser um dos mecanismos pelos quais surgem e se consolidam as diferenças interindividuais nas populações adultas.

Palavras-chave: apego, interação mãe-filhote, cuidado parental, infância, *Sapajus*.

Styles de soins maternels dans les primates : considerations d'une espèce du Nouveau Monde

Résumé: Lorsque nous cherchons à comprendre le comportement humain, les comparaisons avec les primates non humains sont particulièrement pertinentes pour identifier les homoplasies (caractéristiques similaires qui évoluent indépendamment dans différentes espèces). Dans cet article, nous présentons les résultats d'une étude longitudinale de deux ans sur le comportement maternel du Sapajou capucin (*Sapajus* spp.) dans des conditions naturelles. Nos résultats nous ont permis d'identifier différents styles de soins maternels dans un continuum de permissivité à la protection. Nous avons observé que le modèle de lien d'attachement entre la mère et la progéniture suggère que la période de dépendance des bébés singes implique, en plus des processus de maturation physique, l'établissement et le développement de processus psychologiques associés au système d'attachement. Il est possible que la variabilité des styles maternels résultant de la combinaison des caractéristiques de la mère, de la progéniture et du contexte socioécologique, ainsi que l'extension du lien d'attachement, ouvrent la voie à différentes trajectoires de développement. Comme les humains, il peut être un des mécanismes par lequel les différences interindividuelles apparaissent et se consolident au sein des populations adultes.

Mots-clés : Attachement, interaction mère-enfant, soins parentaux, enfance, *Sapajus*.

Estilos de cuidado materno en primates: consideraciones a partir de una especie del Nuevo Mundo

Resumen: Cuando buscamos entender el comportamiento humano, comparaciones con primates no humanos son especialmente relevantes para identificar homoplasias (características similares que evolucionan independientemente en diferentes especies). En este artículo, presentamos los resultados de un estudio longitudinal de dos años sobre el comportamiento materno de monos capuchinos (*Sapajus* spp.) en condiciones naturales. Los resultados permitieron identificar estilos de cuidado materno distintos dentro de un continuo de permisividad a la protección. Se observó que el patrón de desarrollo del vínculo de apego entre madre y cría sugiere que el período de dependencia de la cría de monos capuchinos involucra, además de procesos de maduración física, el establecimiento y desarrollo de procesos psicológicos asociados al sistema de apego. Es posible que la variabilidad de estilos maternos resultante de la combinación de características de madres, crías y contextos socioecológicos, aliada a la prolongación del vínculo de apego, establezca caminos para diferentes trayectorias de desarrollo. Tal como en humanos, este puede ser uno de los mecanismos por los que surgen y se consolidan las diferencias interindividuales en las poblaciones adultas.

Palabras clave: apego, interacción madre-cría, cuidado parental, infancia, *Sapajus*.

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