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Departamento de Psicología FACULTAD DE CIENCIAS HUMANAS

Characterization of Mother-Infant Relationship in Wild Geoffroy's Spider Monkeys (*Ateles geoffroyi*)

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Caracterización de la Relación Madre-Cría en Monos Araña de Geoffroy Silvestres (*Ateles geoffroyi*)

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Abstract

Mother-infant relationships are essential from a development perspective and are particularly relevant in primates as they have a very prolonged period of development. Investigations of primate development have focused primarily on only a few species, with specific social systems and life histories, therefore it is important to extend developmental studies to other primates to have a precise and complete understanding of this phenomenon. I studied mother-infant relationships in Geoffroy's spider monkey (*Ateles geoffroyi*), a New World monkey in danger of extinction that lives in multi-male/multi-female groups of 20 to 50 individuals that fission and fusion into subgroups varying in membership throughout a day. This implies that the infants interact with different members of the group depending on their mother's subgroup, which could have important effects on their behavioral development, especially in their socialization process. In addition, spider monkeys are an interesting model to study mother-infant relationships because of their exceptional slow developmental period, compared with other primates of similar size, which suggests that the quality of the relationship could be very important in the development of behavioral patterns.

I conducted the research in the protected area of Otoch Ma'ax Yetel Kooh, located in the Yucatan peninsula, Mexico, with a group of monkeys that has been studied continuously since 1997. I focused on 12 dyads composed by all the infants of the group which were ≤3 years and their mothers. I used 15-min focal sampling and 20 min scan sampling, with an ethogram of 37 measures associated with mother-infant interaction and infant independent behavior. Data collection was carried out from August 2016 to April 2017. I collected 655 focal observations that covered 149.64 observation hours and 1,069 scans within approximately 770 hours of field work.

Data were analyzed with R version 3.4.0, using lineal mixed models, in which I included age as the predictive variable, and group tenure of the mothers, and sex of the infants as control variables. Age had a significant effect ($p \leq .05$) over a variety of measures of mother-infant relationship and infant behavior. The distance between mothers and infants, and the proportion of time in exploration and social proximity increased with age. Also, independent locomotion increased from 9 to 19 months of age, which was followed by a peak on the rate of bridges around 20 months of age. Social play also reached a peak about this age. Thus, two crucial periods of independence were found before the first and the second years of age.

The study showed that mother-infant relationships in wild spider monkeys are characterized by extended and slow periods of dependency and behavioral development when compare to primate species of similar or greater size. This was interpreted in the light of the different hypotheses that have been proposed to explain slow life histories. Finally, a gradual and soft transition toward infant independence was identified in the mother-infant dyads of the study, which was analyzed in the context of the risk that the ecological and social characteristics of the species could represent to the infant.

Key words: mother-infant relationships, spider monkeys, *Ateles geoffroyi,* behavioral development, life histories.

Resumen

La relación madre-cría es esencial desde una perspectiva del desarrollo y es particularmente relevante en primates dado su prolongado periodo de desarrollo. Los estudios sobre desarrollo primate se han centrado en ciertas especies con sistemas sociales e historias de vida particulares, por lo que es importante extenderlos a otros primates para comprender de una manera más precisa y completa este fenómeno. Por ello, estudié las relaciones madre-cría en el mono araña de Geoffroy (*Ateles geoffroyi*), un mono del nuevo mundo en peligro de extinción que vive en grupos multi-macho/multi-hembra de 20 a 50 individuos, los cuales se dividen en subgrupos que cambian frecuentemente de tamaño y composición a lo largo del día. Esto implica que el infante interactúa con diferentes miembros del grupo dependiendo del subgrupo en el que se encuentra la madre, lo que puede tener efectos importantes en el desarrollo comportamental de los infantes y especialmente en su proceso de socialización. Adicionalmente, los monos araña son un modelo de estudio interesante para estudiar la relación madre-cría debido a su excepcionalmente lento periodo de desarrollo, en comparación con el de otros primates de tamaño similar. Esto sugiere que la calidad de la relación puede ser muy importante en el desarrollo de los patrones comportamentales de esta especie.

Realicé el estudio en la reserva Otoch Ma’ax Yetel Kooh, localizada en la península de Yucatán, México, con un grupo de monos que ha sido estudiado continuamente desde 1997. Me centré en 12 diadas compuestas por todos los infantes del grupo que tenían ≤ 3 años y sus madres. Usé la técnica de muestreo focal con una duración por sesión de 15 min, así como muestreo instantáneo de 20 min. El etograma consistió en 37 medidas asociadas a la relación madre-cría y el comportamiento independiente del infante. Realicé la recolección de datos desde agosto de 2016 hasta abril de 2017, tiempo en el cual recolecté 655 focales, que sumaron 149.64 horas de observación, y 1,069 muestreos instantáneos en aproximadamente 770 horas de trabajo de campo.

Los datos fueron analizados con R, versión 3.4.0, a partir de modelos lineales mixtos, en los que incluí la edad como variable predictora, y el tiempo de permanencia de la madre en el grupo, así como el sexo de la cría, como variables control. La edad tuvo un efecto significativo ($p \leq .05$) sobre varias de las medidas asociadas a la relación madre-cría y el comportamiento del infante. La distancia entre madres y crías, y la proporción de tiempo en exploración y proximidad social aumentaron con la edad. Así mismo, la locomoción independiente incrementó de los 9 a los 19 meses de edad, lo que estuvo seguido de un pico en la tasa de puentes alrededor de los 20 meses de edad. El juego social también alcanzó un pico a esta edad. Así, dos periodos de independencia cruciales se encontraron antes del primer y segundo año de vida.

Como se esperaba, el estudio mostró que las relaciones madre-cría en monos araña silvestres están caracterizadas por periodos de dependencia y desarrollo comportamental largos y lentos en comparación con especies primate de tamaño similar o mayor. Esto fue interpretado a la luz de las diferentes hipótesis que han sido propuestas para explicar las historias de vida lentas. Finalmente, una transición gradual y suave hacia la independencia del infante fue identificada en las diadas madre-cría del estudio, la cual fue analizada en el contexto del riesgo que las características ecológicas y sociales de la especie representan para el infante.

Palabras clave: relación madre-cría, monos araña, *Ateles geoffroyi*, desarrollo comportamental, historias de vida.

Characterization of Mother-Infant Relationship in Wild Geoffroy's Spider Monkeys (*Ateles geoffroyi*)

Tinbergen (1963) presented a framework for studying behavior from four different perspectives to obtain a more complete understanding of animal behavior. A key contribution of Tinbergen's four perspectives was development. In order to address the nature-nurture debate between biologists and psychologists, Tinbergen (1963) proposed that the focus of research should be on the ontogenetic changes in behavior patterns (Crews & Groothuis, 2005).

The idea of development as a determinant to explain behavior has been shared by many biologist and psychologists, and has led to a productive research area (Hogan & Bolhuis, 2005). In concordance with this perspective, some have suggested that behavioral patterns of the organisms are the product of its ontogenetic history and because of that it is necessary to understand the development of behavior to be able to explain it (e.g., Gottlieb, 1983). Today, the systemic theories of development firmly defend the previous ideas and suggest that development in each ontogenetic stage is formed by the results of the development of the previous stages, which also depend on the mutual relationship between the organism and the environment (Griffiths & Tabery, 2013). These views are supported by a body of evidence that shows that early experience has key role in the adult form of behavioral patterns (e.g., Kuo, 1967).

In mammals and particularly in primates the mother is the main stimulus that interacts with individuals in its earliest stage (Lonsdorf & Ross, 2012). Infants of this order are highly dependent on their mothers when they are born and dependency lasts very long (Nash & Wheeler, 1982). Primate mothers are essential to infant development in terms of food, warmth, transportation, stimulation, protection and contact comfort (Fairbanks, 2003; Nicolson, 1991). Because of that, newborn primates remain in permanent contact with their mothers, who usually carry them for transportation (*clinging-carrying pattern*, Rosenblatt, 1998). With time, infants become more independent, increasing their distance from their mothers, who continue to monitor their offspring for many months and even years (Numan, 2015). Therefore, the mother is central in the biological and psychological development of primate infants (e.g., West & King, 1987) and the concept *maternal effects* has been proposed to acknowledge this phenomenon (see Maestripieri & Mateo, 2009). Some evidence of the existence of maternal effects is that the quality of the relationship between mother and infant can influence the psychobiological systems of infants (Kraemer, 1992; McKenna, 1990), and in turn their behavioral and social competence (see Fairbanks, 1996; Suomi, 1997).

Origins of Mother-Infant Relationship Research

Studying mother-infant relationships is essential to understand primate behavioral patterns. One of the first authors that noticed this need was John Bowlby (1969). Bowlby emphasized the effects of early experience in the development of personality and emotional disturbance, focusing on the dynamics of the family itself, and mainly on the relationship between mother and child (Bretherton, 1992). Thus, for Bowlby (1951) the importance of the mother was such that he gave her the role of *psychic organizer*.

Even though Bowlby's theoretic perspective arose from working with children in a clinical environment, he adopted an evolutionary and particularly an ethological framework to formulate his *attachment theory* (Bretherton, 1992). Thus, Bowlby (1958) proposed that attachment behavior was composed of instinctive responses such as suckling, clinging, following, crying and smiling, and was characterized by the search for proximity to one or some significant others, mostly the principal or secondary caregivers.

Robert Hinde was the fundamental figure that helped Bowlby in his approach to the ethological field (van der Horst, van der Veer, & van IJzendoorn, 2007). Thanks to this relationship Hinde developed further research on attachment theory in rhesus monkeys (*Macaca mulatta*; Hinde, 1991), which provided useful methodological and theoretical bases that are still used in this line of research (Hinde & Spencer-Booth, 1968). His main contributions were to study mother-infant relationships in a dynamic perspective, taking into account the social context in which it takes place, and to provide quantitative measures to study this phenomenon in a naturalistic way (Hinde, 1974).

Hinde also established contact between John Bowlby and Harry Harlow (van der Horst, LeRoy, & van der Veer, 2008), who although coming from a different perspective from his European counterparts, developed an experimental line of research with macaques which showed that the bond between mother and infant was not fundamentally dependent on nutrition, but on other needs such as contact, comfort and protection (Harlow, 1974).

Within this context, around the 1960s and 1970s researchers from different disciplines started to study mother-infant relationships in human and non-human primates (Fairbanks, 2003; Maestripieri, 2003). Although they had different backgrounds, all shared a similar theoretical framework based on attachment theory. Unfortunately, this interdisciplinary effort ended quickly (Maestripieri, 2003), and now the studies of human attachment form a separate line of research from the studies of non-human primate attachment (Carrillo & Gutiérrez, 2000; Kondo-Ikemura & Waters, 1995).

Within the nonhuman primate studies, most of the subsequent research followed the path established by Hinde and collaborators with captive rhesus monkeys (Maestripieri, 2003). They defined the quantitative changes of mother-infant contact and proximity through development (Hinde & Spencer, 1971) and developed what is known as the Hinde Index, which is used to quantify the relative contribution of mother and infant to the maintenance of contact or proximity (Hinde & Atkinson, 1970).

From their research with captive rhesus macaques we now know that mother-infant dyads stay almost all the time in ventral contact within the first month of life, but start to break and reestablish contact with their infants since their first week of life (Hinde & Spencer-Booth, 1971). These first interruptions of contact are followed by distress calls of infants (Maestripieri, 1994b, 1995). From the second week of life, infants start to break contact and leave their mothers, exploring the nearby environment (Hinde & Spencer-Booth, 1971). Mothers are primarily responsible for maintaining contact with their infants until 6 weeks of life, when both parties have an equal stake in maintaining contact (Hinde & Atkinson, 1970). At this point infants start to explore more their physical and social environment using the mother as a secure base. For example, Maestripieri and Call (1996) showed that distress indicators emitted by infants when lost or injured by others ceased when contact was reestablished. Between the second and third months of life infants start to take principal responsibility for maintaining contact with their mothers (Hinde & Atkinson, 1970). Suomi (1999) suggested that this was related to an emergence of fear to others, but no evidence to supports this has been published (Maestripieri, 2003). Since this stage, contact is less promoted by mothers and mother-infant conflict for contact and suckling begins (Hinde & Spencer-Booth, 1967; van de Rijt-Plooij & Plooij, 1987).

Similar patterns of change of mother-infant relationships have been described in wild populations of nonhuman primates such as vervet monkeys (*Chlorocebus aethiops*; e.g., Hauser & Fairbanks, 1988), rhesus macaques (e.g., Berman, 1990) and baboons (*Papio anubis*; Lycett, Henzi, & Barret, 1998).

Interspecific Differences in Mother-Infant Relationships

The patterns of change of mother-infant relationships are not the same within the members of the same species (Fairbanks, 2003) and these qualitative differences have been named *maternal styles* (Fairbanks, 1996). This started when Hinde and Spencer-Booth (1971) found that maternal differences with respect to contact initiation were correlated with differences in caregiving behaviors, and the same thing happened between maternal rejection and the proportion of time that mother and infant were out of contact. In a subsequent study, Hinde and Simpson (1975) confirmed that these two groups of behaviors vary independently.

Later, Fairbanks and McGuire (1987) used principal component analysis to analyze data taken from a captive population of vervet monkeys and found two factors associated with maternal care: rejection (related to breaking ventral contact, leaving and rejecting the infant) and protectiveness (related to approaching, making ventral contact, restraining, grooming and inspecting the infant). Therefore, they proposed that mother-infant relationships can be categorized as maternal styles accordingly: controlling (high protectiveness and high rejection); protective (high protectiveness and low rejection); rejecting (low protectiveness and high rejecting); or laissez-faire (low protectiveness and low rejection).

Interestingly, maternal styles influence the development of behavioral patterns such as reaction to novelty (Fairbanks & McGuire, 1988), response to conspecifics (Fairbanks & MacGuire, 1993) or future maternal behavior (Fairbanks, 1989). For example, Bardi and Huffman (2002) found that infants of protecting mothers tend to explore the environment less than infants of mothers with other maternal styles, and that infants of rejecting mothers were more likely to interact with others. The authors concluded that rejecting maternal styles tend to encourage infant independence, while protective maternal styles delay it. Unfortunately, little research has focused on understanding the developmental consequences of varying mother-infant relationships (Roney & Maestripieri, 2003).

It is yet unclear what factors could explain the qualitative differences observed in mother-infant relationships, but some aspects have been proposed to understand them. Variables associated with the mother, such as maternal experience (e.g., Hooley & Simpson, 1981), rank (e.g., Altmann & Samuel, 1882), or age (e.g., Berman, 1984) could have an effect on the quality of maternal styles. For example, Schino, D’Amato, Mari, and Troisi (1995) found that with increasing age mothers were less protective with their infants. In addition, a negative effect of extremely young mothers rearing their infants has been found. Basically, infants of adolescent mothers have high mortality rates, which could be related to the fact that these mothers are usually neglecting and extremely rejecting with their infants (Fairbanks, 2003).

Furthermore, many studies showed that factors associated with the infant, mainly the sex (e.g., Nguyen, Gesquiere, Alberts, & Altmann, 2012), cause differences in the quality of mother-infant relationships. In this respect, it was recently reported that rhesus mothers were more aggressive toward their sons within the first year of life (Kulik, Langos & Widdig, 2016). Authors interpreted this difference as mothers developing weaker bonds with infant males, which supports that mothers promote more their relationships with the philopatric sex of the species (in this case the female but in other species the male, e.g., Murray et al., 2014), which could be a proximate cause of juvenile dispersal.

Finally, there are studies which showed that factors associated with the social (Maestripieri, 2001) or ecological environment (Rosenblum & Andrews, 1994) can produce differences in the way mothers and infants interact. In a study by Maestripieri (2001), he found differences in the maternal styles between two groups of captive rhesus macaques, which differ in their social density. The mothers of the high social density group were more protective with their offspring than the mothers of the less dense group, which seems to be caused by infants experiencing a higher risk (e.g., kidnapping) in the first population.

Inter-Species Differences in Mother-Infant Relationships

Primate species vary considerably in terms of their ecological niches and social systems, which would suggest interspecies differences in mother-infant relationships (e.g., Fairbanks & McGuire, 1987). As expected, mother-infant relationships are highly diverse among primates (Maestripieri, 1994a). For example, according to Hinde and Simpson (1975), rhesus macaques have a controlling maternal style, characterized by high protective behavior and high rates of rejection. Conversely, stumptail macaques (*M. arctoides*) are characterized by laissez-faire styles, showing low protectiveness and rejection with their infants (Altmann, 1980; Maestripieri, 1994b). These differences seem to be related to the species-typical social structure and dominance hierarchies (Maestripieri, 1994b). While rhesus macaques have a lot of interspecific aggression, with little social tolerance and very infrequent affiliative behaviors, stumptail macaques present many affiliative interactions that reduce social tension (de Waal and Luttrell 1989; Thierry, 1990). Given the difference in social structure between species, rhesus mothers need to be more controlling with their infants to protect them from aggression, but also to reject them when they are young so they can develop self-protection skills (Maestripieri, 1993).

Thus, Maestripieri (1993, 1994b) has proposed that differences in maternal styles between species are strongly related to social structure and dominance hierarchy because it directly affects the degree of risk for an infant. Supporting this hypothesis, mothers of egalitarian species, which have more affiliative behaviors, are less protective and less likely to reject their infants than mothers of despotic species, which have more agonistic behaviors and less affiliative ones (Maestripieri, 1994b). In addition, Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), another egalitarian species, have a maternal style characterized by low restrictiveness and low rejection (Li, Ren, Li, Zhu, & Li, 2013).

However, Maestripieri (1994a) emphasizes the need to consider the interaction between the infants and the other members of the group to understand properly the relation between social context and maternal styles, and suggests that the structure and function of infant handling in each species is the best indicator of this interaction. For example, in stumptail macaques, infants experience low risk because of the benign interactions that others have with them, which in turn explain the relaxed and detached mothering styles of this species (Maestripieri, 1994a).

An investigation on maternal styles of bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*; de Lathouwers & van Elsacker, 2004) revealed three factors from a principal component analysis: protectiveness (high episodes of making contact, approaching, restraining, and high ventral contact durations), distance (high episodes of breaking contact and leaving), and refusal (high rates of reject and nipple reject). Data showed that both species had similar scores in protectiveness, but bonobo dyads had higher scores of refusal than chimpanzees. This was explained by an attempt by bonobo mothers to regulate the end of nursing, given the longer interbirth intervals of captive bonobos compared to captive chimpanzees, or as a way to control that nursing does not hinder other activities, especially social activities, due to their higher social budget in comparison with chimpanzee females. Also, bonobo mothers had higher scores of distance compared to chimpanzees. Chimpanzee mothers broke contact and leaved their infants more often with increasing age, whereas bonobo mothers showed the opposite trend. Lathouwers and van Elsacker (2004) suggested that this could be due to the higher risk of infanticide that immature chimpanzees experience compare to bonobos, which lead mothers not to break contact with their infants when they are young but then promote their distance to help them achieve independence.

The Spider Monkey as a Model for Studying Mother-Infant Relationships

Given the importance of mother-infant relationships in understanding primate development, it has received considerable research attention (see Fairbanks, 1996, 2003; Maestripieri, 2003). However, the focus has been primarily in Old World primates, and especially olive baboons (*Papio anubis*, e.g., Altmann, 1980), vervet monkeys (*Chlorocebus aethiops*, e.g., Lee, 1984) and different macaque species (e.g., *Macaca* *mulatta, M. fascicularis y M. tonkeana,* Thierry, 1985). There are relatively few studies conducted on New World monkeys, and most have been done with captive monkeys (tufted capuchins [*Cebus apella*] and squirrel monkeys [*Saimirí sciureus*], Fragaszy, Baer, & Adam-Curtis, 1991; cotton-top tamarin [*Saguinus oedipus*], Cleveland & Snowdon, 1984; red-bellied titi monkeys [*Callicebus moloch*], Hoffman, Mendoza, Hennessy, & Mason, 1995; common marmoset [*Callithrix jacchus*], Arruda, Yamamoto, & Bueno, 1986; and owl monkeys [*Aotus trivirgatus*], Dixon & Fleming, 1981).

Given the social and ecological differences of primate species, there is likely a high degree of variation in mother-infant relationships within this order (e.g., Lathouwers & van Elsacker, 2004; Maestripieri, 1994a; Thierry, 1985). Most species of Old World monkeys live in large and cohesive groups, in which females are the philopatric sex. However, this social system is not shared universally among monkey species. For example, Geoffroy’s spider monkey (*Ateles geoffroyi*), a New World monkey, lives in groups of 20 to 50 individuals that fission and fusion throughout a day in fluid and smalls subgroups, according to their activities and resource availability (Aureli & Schaffner, 2008).

The term fission-fusion dynamics is used to refer to different degrees of cohesion between the members of a group, thus, it is characterized as: “the extent of variation in spatial cohesion and individual membership in a group over time.” (p. 628, Aureli et al., 2008). The high levels of fission-fusion dynamics experienced by spider monkeys are shared by few primate species such as chimpanzees, geladas (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*) and humans, and by other mammals such as bats (*Chiroptera spp.*), dolphins (*Delphinidae spp.*), elephants (*Loxodonta spp.*), and spotted hyenas (*Crocuta crocuta*; Aureli et al., 2008).

Spatiotemporal variation promotes certain types of social interaction (Aureli et al., 2008), which could have important effects on mother-infant relationships and infant behavioral development, given that social companions can be selected by the mother and this could likely influence the social behavior of infants (Watts & Pussey, 2002). This is very important taking into account that beside of mother-infant relationships, parents can influence the social development of infants through their own interactions with others (Roney & Maestripieri, 2003).

Female spider monkeys are characterized by being less social than males (Slater, Schaffner, & Aureli, 2009), which could be related to the fact that males are largely the philopatric sex (Aureli, Di Fiore, Murillo-Chacon, Kawamura, & Schaffner, 2013). Although sex differences in spider monkey's behavior are evident and have been reported (see Slater et al., 2009), it is not clear how these sex specific behavioral patterns are shaped through infant development (Vick, 2008). Thus, it is possible that the mother's selection of social companions could affect infant development and explain some of these differences. In a study done with chimpanzees, who have also high degrees of fission-fusion dynamics and males are the philopatric sex, Murray et al. (2014) found that mothers of male infants spent more time with other group members and were part of larger subgroups than mothers of female infants. According to the authors of the study, this appears to be related to later sex differences in the social behavior of this species: with males being more likely to engage in social interactions (Mitani, 2009).

In contrast to the most commonly studied species in primate developmental research (e.g., Kulik et al., 2016), it is possible that spider monkey mothers invest more in their male infants. Symington (1987a) suggested this with *Ateles belzebuth chamek*. She found that compared to female infants; male infants have longer interbirth intervals after birth (36 versus 29 months). Vick (2008) research showed a similar result with *A. geoffroyi*, but only in the more habituated group of her study: after the birth of male infants, interbirth intervals were slightly longer (36 versus 33.6 months). When the data were combined with the one of the other, larger group, such a difference was not present.

Spider monkeys are also an intriguing model for studying mother-offspring relationships because of their slow developmental rate, compared with other primates of similar size (see Appendix; Chapman & Chapman, 1990). Wild female spider monkeys reach sexual maturity at approximately 4-5 years of age, have gestation periods of 226-232 days, and interbirth intervals of 28-36 months (Campbell & Gibson, 2008; Vick, 2008). In addition, usually they give birth to one infant, although some cases of twins have been reported (e.g., Link, Palma, Velez, & De Luna, 2006). This suggests that mother-infant relationship in this species could show some differences compared to the maternal styles of other primate species, but also that this relationship could have greater effects on the development of behavioral patterns of the infant spider monkey (Campbell & Gibson, 2008).

The Importance of Studying Spider Monkeys

Ateles genera extend from the south of México to Bolivia; however, spider monkeys are relatively little studied in their natural environment compared to other New World monkeys such as capuchin monkeys (*Cebus spp.*) or howler monkeys (*Allouatta spp.*; Campbell, 2008). This is because it is very difficult to observe spider monkeys given their fast locomotion, which mainly occurs in the upper branches of trees, and due to the high degree of fission-fusion dynamics present, which does not allow the possibility to follow big groups in one single moment (Campbell, 2008).

Since 1982 the species *Ateles geoffroyi* is on the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) as vulnerable species and from 2008 as species in danger of extinction, categories that conceive the viability of its subsistence by the implementation of conservation strategies, derived in great deal from behavioral and ecological research. Furthermore, the IUCN in conjunction with the International Society of Primatologists declared *Ateles geoffroyi* one of the 25 most endangered primates on the planet (Joint meetings of the ISP and ASP meetings, 2016, Chicago, Illinois).

Species that have low population sizes, occupy big ranges of territory, have low rates of fecundity, and depend on irregular and unpredictable resources, are at risk to extinction by habitat fragmentation (Meffe & Carroll, 1994). This is the case of the *Ateles* genera. They are often found at very low population densities, especially in Latin-American jungles (e.g., Perú; Symington, 1987a), occupy large home ranges between 1.5 to 3.9 km^2 (Klein & Klein, 1977), and have a slow rate of reproduction and long life histories (Campbell & Gibson, 2008). Finally, spider monkeys are a frugivorous species, which rely on mature fruiting trees (Di Fiore, Link, & Dew, 2008). Therefore, they require home ranges with a high diversity of fruit trees that is difficult to found given habitat loss and degradation (Ramos-Fernández & Wallace, 2008). Thus, studying the behavior of this species is fundamental to be able to develop conservational alternatives to prolong the existence of Geoffroy's spider monkeys. Developmental studies are particularly relevant with this respect given the long interbirth interval and the late sexual maturity of the species (Campbell & Gibson, 2008), which make evident the importance of achieving successful developmental trajectories to prevent the extinction of the species.

Aims and Study Rationale

The general aim of my thesis was to characterize mother-infant relationships in wild *Ateles geoffroyi* in a systematic and quantitative way. In general, behavioral development in primates has received little attention and in the case of spider monkeys, except for brief descriptions (e.g., Eisenberg, 1976; van Roosmalen, 1985; van Roosmalen & Klein, 1988), there is almost no literature available. For example, there is a clear picture of the behavioral development of macaques (Suomi, 1999), whereas little is known about spider monkeys (Defler, 2010). The most prolonged study of infant development in this order was done by Vick (2008). In her research some events of the life history of immature spider monkeys were analyzed, such as association patterns and maternal investment, and some measures of mother-infant relationships were taken (e.g., approximate distance between mothers and infants through development). Vick's (2008) research was not focused on the dynamic development of this relationship and its role in the behavioral patterns of infants. The work of Rodrigues (2007) was also an important contribution, but it primarily focused on sex differences in juvenile social behavior of wild spider monkeys. Therefore, I wanted to explore the changes of mother-infant relationships in this species throughout the first 3 years of life, and to analyze the development of infant behavior within this period. I expected that age would have an effect over mother-infant interactions and infant development, and more specifically that data would show that spider monkey infants have a late behavioral development compared to other primate species of similar size, particularly in terms of their independence from the mother.

Method

Study Site

I carried out the study in the protected area of Otoch Ma'ax Yetel Kooh (OMYK), located in the Yucatan peninsula, Mexico, adjacent to Punta Laguna village in the state of Yucatan. Since 1997 a long-term study of the ecology, conservation and behavior of Geoffroy's spider monkeys (*Ateles geoffroyi*) has been ongoing (for a detailed description of the study site see Ramos-Fernández & Ayala-Orozco, 2003). The protected area of 5,367 ha includes mature forest (25%) and different grades of regenerating forest (8 to 50 years, Ramos-Fernández et al., 2011).

OMYK was founded in 2002 as a natural area protected by the federal government. As its Mayan name indicated (in English "the house of the spider monkey and the cougar"), this area constitutes an important habitat Geoffroy's spider monkey, which conservation is one of the main objectives of the federal government. The Yucatan peninsula consists of forests of different stages and degrees of fragmentation, which represents the principal threat to the existence for the Geoffroy's spider monkeys that live in this habitat (Ramos-Fernández & Ayala-Orozco, 2003). However, in a review done by Ramos-Fernández et al. (2011), in terms of population density, group sized tendencies and reproductive rates; OMYK seems to have great value as a conservation area of biodiversity.

Thus, since its foundation, OMYK has constituted a field site to permanently study Geoffroy's spider monkeys, which makes it the longest conservation and research project for this species or any species of spider monkey (Ramos-Fernández et al., 2011). The monkeys of the reserve are habituated to the presence of humans thanks to research and touristic activities, which makes observation easier and it is and ideal study site to develop studies which allow the understanding of the behavioral patterns of the species.

Subjects

I conducted the study on the Eastern study group of OMYK that has been followed for 20 years, 4-8 hours per day, 4-6 days per week, by local assistants and students. At the beginning of data collection the group comprised 38 monkeys, but during the study period two infants were born, one disappeared and an adult female joined the group.

All monkeys were individually recognized (Table 1). In this genus individual identification is based on morphological characteristics such as pelage coloration, face characteristics, and size, shape, coloration and pattern spots of genitals (Campbell & Gibson, 2008; Vick, 2008). Female spider monkeys are characterized by a large clitoris, even when infants (Campbell & Gibson, 2008), and nulliparous females can be distinguished by the absence of prominent nipples and by the presence of non-flattened pelage in the area, usually caused by nurturing (Vick, 2008). In contrast, adult males can be distinguished by the presence of totally descended testicles.

To classify the members of the group, I use the four developmental stages usually employed in primate studies: (a) infants, (b) juveniles, (c) subadults, and (d) adults. For Lonsdorf and Ross (2012) the key criterion to define infancy is that offspring are nutritionally dependent on mothers. Following Pereira and Altmann (1985), juveniles are characterized as individuals that have gone through a weaning process but have not yet reached puberty or show any reproduction event. Subadults are reproductively competent, but have not reached full body size.

In her study with spider monkeys, Vick (2008) categorized infants as individuals that still nurse and are mainly carried by their mothers to move around; juveniles as subjects that have one subsequent sibling and subadults are monkeys that have at least two siblings or began to spend a lot of time with other adult males. Shimooka et al. (2008) proposed the following criteria for defining age classes: (a) infants: less than 2 years; (b) juveniles: 2 to 5 years; (b) subadults: 5 to 8 years; (c) adults: more than de 8 years. I use the same classification except for infants, taking into account the weaning criteria for defining infants (Pereira, 2002). Although in the first studies of spider monkeys the age at weaning was considered around 2 years (Symington, 1987b), some researchers have observed nursing at later stages. For example, Vick (2008) found that the earliest weaning occurred at 24 months and the latest at 31 months. This variation is related to the interbirth interval, which in this population is 36.6 months (Vick, 2008). Thus, for my study I considered infants from 0 to 3 years. Table 2 presents information of the 12 infants and their mothers, specifying the age of the infant and some characteristics of the members of the dyad that served as control variables in data analysis.

Table 1. *Group composition at the end of the study in terms of sex and age classes.*

	Adult	Subadult	Juvenile	Infant	Total
Males	4	2	3	5	14
Females	14	1	5	7	27
Total	18	3	8	12	41

Table 2. *Mother-infant dyads ordered by age of the infant and relevant characteristics of the infant (sex and range of age during data collection) and the mother (group tenure since immigration and number of previous offspring).*

		Infant characteristics		Mother characteristics	
Infant	**Mother**	**Sex**	**Range of age during data collection (in months)**	**Group tenure (in years)**	**Number of offspring**
Ek	Mich	F	1-2	1	1
Sacbé	Joanne	F	1-4	12	5
Valentín	Verónica	M	7-14	26[a]	8
Morita	Mandíbula	F	9-16	3	2
Xtabai	Pancha	F	13-19	5	2
Estrella	Lola	F	19-26	15[b]	3
Panty	Tángara	F	19-26	5	2
Francis	Hilda	F	21-28	6	2
Nacho	China	M	22-29	26[a]	8[c]
Daniel	Flor	M	28-35	26[a]	8[c]
Apolo	Antena	M	32-36	3	1
Andrés	Joanne	M	34-36	12	4

Note: [a] = minimum group tenure given that these females were already in the group at the beginning of the long-term project in 1997. Five years before the 1997 were added to the duration of the project period to provide a conservative age estimate as it is the mean female migration age in this species (Symington, 1988; Campbell & Gibson, 2008) and in this specific population of spider monkeys (Vick, 2008). [b] = the female was born in the study group and did not emigrate. [c] = known offspring since 1997.

Procedure

Fieldwork was carried out from August 2016 to April 2017. During the first month I developed and refined the ethogram, and recognized the study subjects. I carried out observations between 6:00 and 18:00 hours. As spider monkeys practice a high degree of fission-fusion dynamics (Aureli & Schaffner, 2008), not all subjects could be sampled every day. However, at the beginning of the study I selected a sampling order each day according to a random list previously prepared and after a few weeks I tried to prioritize sample subjects with the fewest observations.

I used 15-min focal sampling (Altmann, 1974). To ensure representative data, I sampled subjects no more than once per hour and three times per day. I terminated observations if the infant was out of view for more than 5 minutes continuously or in total during the focal sample. At the beginning of each focal sample, I recorded the date, hour, members of the dyad and identities of the other subgroup members. Observations were recorded with a digital voice recorder and later transcribed into a Microsoft Excel file.

The ethogram was based on 37 behaviors typically used in investigations related to mother-infant relationships in primates (e.g., Deng & Zhao, 1991; Schino et al., 1995) and primate infant development (e.g., Rhine & Hendy-Neely, 1978). I also incorporated behaviors previously used by spider monkey researchers (e.g., Eisenberg, 1976; Schaffner & Aureli, 2005; Vick, 2008; Youlatos, 2008) and additional behaviors observed in the pilot study (Table 3). I divided measures into three categories: mother-infant interaction, independent infant behavior and social infant behavior. If applicable, I recorded initiators and receptors of all interactions. For behavioral states, I recorded the duration and for behavioral events the frequency.

For each focal, I recorded the initial and final distance between mother and infant in each session according to four classes: 0-1 m, 1.1-3 m, 3.1-8 m, and < 8 m. Furthermore, I recorded the activity of the mother during focal observations as follows: (a) feeding: the mother explores visually, handles and/or places potential food into her mouth; (b) resting: the mother sits or lies in one spot without eating; (c) travelling: the mother moves (at least from one tree to the other) walking, jumping, running or climbing.

I also performed scan sampling (Altmann, 1974) before the first focal sample of the day and throughout the day with 20 min intervals. I registered the range of distance between all infants present and their mothers, and the presence of any of the following: grooming, nipple contact, ventro-ventral contact, gross body contact, extremity contact, external contact, social proximity, external grooming, sexual behavior and/or social play. If the subjects were not present or a focal was in course, the scan sampling was skipped until the next sampling time.

Table 3. *Ethogram*

Mother-infant interaction	**Definition**
Nipple contact*	Infant in oral contact with the mother's nipple, except when it is rejected (Deng & Zhao, 1991; Hinde & Spencer-Booth, 1968; Lee, 1984; Nash, 1978). [a]
Ventro-ventral contact*	Infant ventral surface is in contact with mother's abdomen (Li et al., 2013). It includes nipple contact.
Gross body contact*	Any physical contact between dyad members, including nipple contact, ventro-ventral contact and extremity contact. Brief touches are not included (Bardi & Huffman, 2002).
Extremity contact*	Infant in physical contact with the limbs of the mother (including the tail). Only recorded when it is not accompanied by any other kind of contact (Murray & Mayer, 1977). [a]
Approach	The mother/infant moves within a distance of less 1 m from the other member of the dyad (Deng & Zhao, 1991; Schino et al., 1995; Vick, 2008).
Leaves	The mother/infant moves away from a distance of less 1 m from the other member of the dyad (Deng & Zhao, 1991; Schino et al., 1995; Vick, 2008).
Breaks contact	Mother/infant ends physical contact with the other member of the dyad moving away. [a]
Breaks ventro-ventral contact	Mother/infant ends ventro-ventral contact with the other member of the dyad moving away. [a]
Grooming*	The mother/infant uses her hands or mouth to manipulate the fur of the other member of the dyad (Schaffner & Aureli, 2005). A new grooming state is recorded when there is a break between one episode and the next of at least 5 s (Maestripieri, 2002).
Dorsal carry*	Infant is on the mother's back while the mother moves, hangs or stands.
Ventral carry*	Infant is on the mother's ventral side while the mother moves, hangs or stands.
Grooming request	Mother/infant goes next to the other member of the dyad and lies with the arm stretched above its head, letting the front, back or lateral side of the body

	exposed. [a]
Aggression	Mother bites, hits, pushes or threats the infant (Nash, 1978). Not recorded in cases when mother prevents the infant to access the nipple with the mouth.
Reject	Mother prevents the infant to take the nipple with its mouth, moving away from it, sitting with unavailable nipples after an infant approach or threating, pushing or biting the infant (Deng & Zhao, 1991; Nash, 1978; Schino et al., 1995).
Retrieval	The mother approaches to the infant, carries it and gets it away of what it is doing (Förster & Cords, 2002; Nash, 1978).
Restrain	Mother prevents the infant to breaks physical contact with it, holding the infant with her hands when the infant makes locomotion attempts (Deng & Zhao, 1991; Schino et al., 1995).
Body bridge	Behavior that facilitates infant crossing of canopy gaps. Mother establishes a secure hold of branches at one side of the gap with hind limbs and tail and pulls her body across the gap holding branches with her forelimbs with variables bodily orientation (Youlatos, 2002; Youlatos, 2008). This variable is only register when the bridge is used by the infant to go over the gap.
Branch bridge use	While travelling, the mother grabs and pulls a branch toward the infant. Then, the infant uses the branch to bridge to gap and continue travelling.

Infant solitary behavior	**Definition**
Exploration*	The infant touches, manipulates, licks, smells or introduces objects in its mouth (e.g., branches or fruits; Bardi & Huffman, 2002). It is specify if the object is some potential food.
Locomotion*	Infant walks, runs, jumps or climbs (Bardi & Huffman, 2002), while the mother travels.
Scratching	Infant does repeated movements with its hands during which the fingertips are drawn across the infant's fur (Bardi & Huffman, 2002).

Infant social behavior	**Definition**
Social grooming*	A group member other than the mother uses its hands or mouth to manipulate the fur of the infant, or vice versa (Schaffner & Aureli, 2005). A new grooming bout is recorded when grooming restarts after a break of at least 10 s or more (Maestripieri, 2002).[a]
Social contact*	Infant is in physical contact with a group member other than the mother for at least 5 s. Social grooming is not considered as social contact.
Social proximity*	Infant is within 1 m from a group member other than the mother for at least 5 s (Nash, 1978), while being 1 m away of the mother. Social contact is also considered social proximity.
Grappling*	Prolonged exchange between two individuals lasting several minutes and may involve facial greeting, face touching, embraces, tail wrapping, pectoral sniffing, and genital contact (van Roosmalen & Klein, 1988)

Sexual behavior*	Infant mounts or is mounted by a group member other than the mother (Nash, 1978).
Social play*	Infant wrest, pull or chase with any group member other than the mother, or vice versa (Bardi & Huffman, 2002; Nash, 1978). A new bout is recorded only when playing restarts after a break of at least 30 s.
External aggression	Any group member other than the mother bites, hits, push or threats the infant, or vice versa (Nash, 1978).
External bridge	Any group member other than the mother makes body or branch bridge (Youlatos, 2002; Youlatos, 2008).
Whinny	Long call of high frequency and extensive frequency modulation (Eisenberg, 1976).

Note: Behavioral states are marked with *. The other measures are behavioral events. ^{a} = Measures that had very low frequencies and did not allowed statistical analyses.

Data Analysis

To study the effect of age of the infant in response variables related to mother-infant interaction and infant behavioral development, I used generalized linear mixed models (GLMM; Baayen, 2008). Although, the sex of the infant and the experience and group tenure of the mother were part of the initial model, those factors were included as control variables. Also, as suggested by Schielzeth and Forstmeier (2009), I fit the model with the identity of the subject and the mother as random effects and with the random slope of age within subject identity to maintain type I error at 5%. First, I fit the models including the interaction between the random slope and the intercept, but it was unidentifiable as indicated by absolute correlation parameters being essentially one, thus I excluded the interaction from the model.

For behavioral states, proportions of time were calculated dividing the total duration of the behavior per infant per month (e.g., total time in gross body contact) by the total observation time (total observation time of that subject in that month). For behavioral events with upper limit, the proportion of events was calculated dividing the number of events per infant per month (e.g., infant approaches) by the total number of events per infant per month (e.g., total approaches). Scan data and proximity measures taken at the beginning and the end of focal were also analyzed in this way. Finally, for behavioral events with no upper limit, rates were calculated dividing the number of events per infant per month by the total observation time (of that subject in that month).

All measures expressed as proportions of time were analyzed as Gaussian, whereas proportions of counts with binomial error structure and logit link function, by using two-column matrix with the number of events/duration of the behavioral state (in minutes) and the total number of events/corresponding observation time (in minutes) as the response (Baayen, 2008). Rates were analyzed with Poisson and log link function, including the corresponding observation time (in minutes and log transformed) as an offset term into the model (McCullagh & Nelder, 1989).

After a collinearity analysis I excluded experience from all models given that it had the highest VIF (higher than 40; Field, 2005) and a correlation of 0.98 with group tenure. Thus, I assumed that including group tenure in the model controlled for the effect of experience. After excluding experience, VIF values for age, sex and group tenure were around 4. Furthermore, all covariates (age, experience and group tenure) were z-transformed (to a mean of 0 and a standard deviation of 1) to make the interpretation of the estimates easier (Schielzeth, 2010). For the rate of bridges and the proportion of time in social play I predicted that age could have a nonlinear effect on the response variable, so the main effect of age was also included to achieve meaningful models.

The models were fitted in R (version 3.4.0; R Core Team 2017) using the function glmer of the R package lme4 (version 1.1-13; Bates, Mächler, Bolker, & Walker, 2015). Confidence intervals were derived by the function bootMer of the same package, using 1,000 parametric bootstraps and bootstrapping over the random effects too (argument ‘use.u’ set to TRUE).

As an overall test of the effect of the age, I compared the full versus the null model using a likelihood ratio test (Dobson, 2002). The null models included the control variables (sex of the infant and group tenure of the mother) and the random effects (Forstmeier & Schielzeth, 2011). When I predicted nonlinear effects, I included age also as a fixed effect.

Finally, model stability was analyzed by comparing the estimates obtained from a model based on all data with those obtained from models with each of the levels of the random effects excluded one at a time.

Results

I collected 655 focal observations (*M*=57.58, *SD*=18.84) which summed 149.64 observation hours (*M*=12.47, *SD*=5.22) and 1,069 scans (M=89.083, *SD*=35.418) within approximately 770 hours of field work. I grouped focal observations into 76 data points which represent one month of age of each infant, but after excluding data points of less than 50 minutes (0.833 hours) to promote representative data, my sample consisted of 65 data points (Table 4).

Table 4. *Number of observation hours per subject per month of age.*

Month of age	**Subject**											
	EK	**SB**	**VL**	**MY**	**XT**	**ES**	**PN**	**FR**	**NA**	**DA**	**AP**	**AS**
1	3.819	1.552										
2	1.852	4.298										
3		2.585										
4		1.000										
7			2.118									
8			2.087									
9			3.784	1.108								
10			1.458	3.247								
11			1.663	2.161								
12			1.428	0.665								
13			5.41	0.898	0.648							
14			2.164	1.776	2.055							
15				3.077	2.112							
16				2.959	2.561							
17					0.432							
18					0.254							
19					0.722	0.638	2.405					
20						2.941	1.580					
21						1.99	2.454	1.494				
22						2.359	0.924	1.585	2.050			
23						0.925	0.983	2.209	1.458			
24						1.386	3.161	0.941	2.264			
25						2.264	2.636	0.247	1.653			
26						5.119	1.318	3.101	1.402			
27								4.036	2.371			
28								1.426	5.038	0.662		
29									0.994	0.675		
30										1.758		
31										1.996		
32										0.937	0.478	
33										1.933	2.153	
34										3.408	0.684	2.340
35										1.829		2.018
36											1.362	2.155

Note: In gray are highlighted the data points with less than 50 minutes (0.833 hours) that were excluded from data analysis.

Contact and Proximity

In the first month of age the two newborns were in ventro-ventral contact more than 80% of the observation time (Figure 1). In newborns, when ventro-ventral contact took place, usually the infant was on the lower part of the mother's belly but often would climb to the upper part of the ventrum and established nipple contact. In the second month infants started to move more around the body of their mothers, mostly alternating between ventro-ventral and dorsal contact. In the third month infants were still more than 50% of the time in ventro-ventral contact (Figure 1). Except for one data point, infants between 4 and 36 months of age spent less than 20% of the time in ventro-ventral contact. No statistically significant effect of age was found regarding this response variable (estimate ± SE=-0.430± 0.334, X^2=1.445, *gl*=1, *p*=.229).

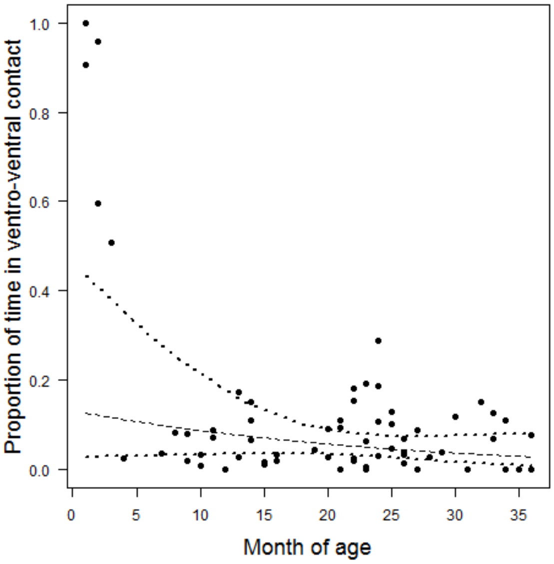

Figure 1. Proportion of time in ventro-ventral contact. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

Reject was registered in 26 cases during focal observations (73.976% directed toward female infants), with just four cases involving some kind of aggressive behavior, which were usually just facial threats, and in some cases involved chases, soft bites or slaps. Reject usually was manifested as the mother moving away from the infant after it tried to make ventro-ventral contact. No case of pushing was ever seen. The majority of rejects occur when the mother was resting (76.923%), four when she was moving (15.384%) and only two when the mother was feeding (7.692%). Cases of reject were seen between the 19 and 33 months of age of infants (Table 5). Eight cases of aggression from mother to infant were registered during focal observations. Six of those executed in the context of nursing rejection (toward three female infants between 19 and 28 months of age), and two in the context of carrying rejection (toward one female infant of 10 months).

Table 5. *Month of age at first and last reject for each subject (taken from focal samples and adlibitum data).*

Subject	Range of age while data collection	Month of age at first reject	Month of age at last reject
Estrella	19 to 26 months	23	26
Panty	19 to 26 months	19	23
Francis	21 to 28 months	23	28
Nacho	22 to 29 months	25	25
Daniel	28 to 35 months	30	33

During the whole study the newborns were almost all the time in gross body contact with their mothers (Figure 2). The proportion of time in gross body contact gradually decreased during the first year and then maintained stable rate (lower than 40% of the time; estimate ± SE=-0.987±0.342, X^2=5.359, *gl*=1, *p*=.020; Figure 2).

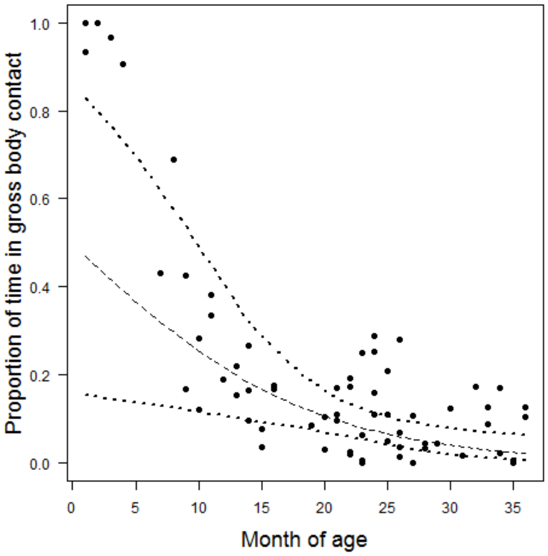

Figure 2. Proportion of time in gross body contact. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

The two newborn infants broke contact from their mothers at the beginning of their third month and move more than one arm's reach from their mothers at the end of 3 months. After this the mother of one infant showed three of the seven cases of retrieval registered in all focal observations. Another three cases of retrieval were seen in the same dyad and within the same context out of focal samples.

Three cases of retrieval occurred during travel when an infant was 8 and 9 months old. The last two cases of retrieval occurred by a mother of a 13 month old male infant, when she took him off the ground. Ground play is common in the immature members of this population. Every time the mother saw her infant playing on the ground, she emitted groans and chips. In those cases it was very common that she went down groaning, very near the ground and if he approached her, she retrieved him. Once she tried to prevent him, unsuccessfully from playing on the ground by holding his tail. Restriction was also observed out of focal time when the same mother took her 6 month old male infant by the tail, not letting him return to an upper branch that he was exploring before. This was observed during the pilot study.

As expected, proximity time between mother and infant decreased throughout development. This was found with regard to the proportion of proximity time during focal observations (estimate ± SE=-1.027±0.318, X^2=6.878, *df*=1, *p*=.008; Figure 3) and when the number of proximity points collected at the beginning and the end of focal observations was modeled as the response variable (estimate ± SE=-1.018±0.377, X^2=5.196, *df*=1, *p*=.023; Figure 4). Scan data revealed the same pattern; a negative effect of age with regard to proximity between the members of the dyad (estimate ± SE=-0.960±0.296, X^2=6.091, *df*=1, *p*=.013). Although some older infants spent less than 10% of observation time near their mothers, in the majority of cases infants of all ages spent more than 20% of the time in proximity with their mothers.

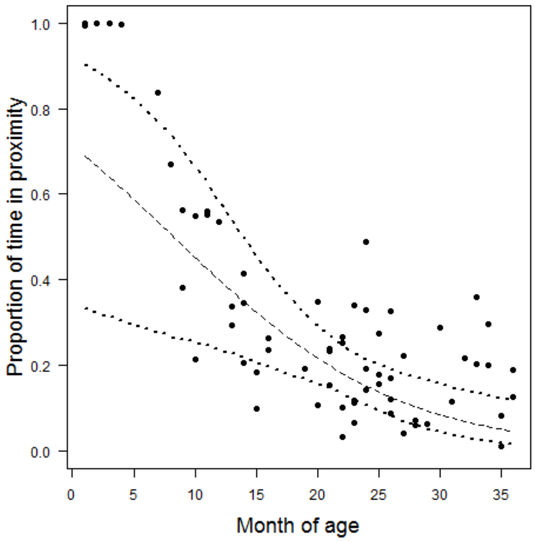

Figure 3. Proportion of time in proximity. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

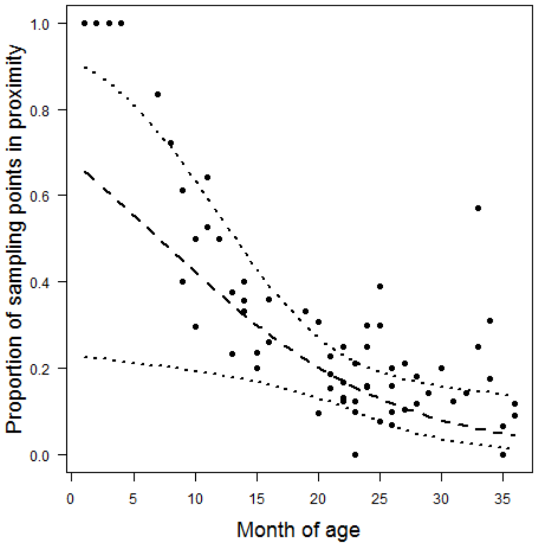

Figure 4. Proportion of sampling points in proximity. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

Additionally, age had a positive effect in the number of sampling points before and after focal observations in which the infant was 8 m or more from the mother (estimate ± SE=1.375±0.284, X^2=11.318, *df*=1, *p*=.001; Figure 5). The same trend arose when scan data were analyzed (estimate ± SE=1.271±0.317, X^2=9.527, *df*=1, *p*=.002). Infants started to be at more than 8 m from their mothers when they reached 13 months of age, but this range of distance was pretty unusual until infants were older than 20 months (less than 20% of sampling points). In one case a male infant at 34 months was even more than 50% of the sampling points before and after focal observations 8 m away from his mother. Furthermore, another male infant of 36 months was not in the same subgroup as his mother. Actually, at 34 months of age, two male infants were seen more than 20 m away from their mothers.

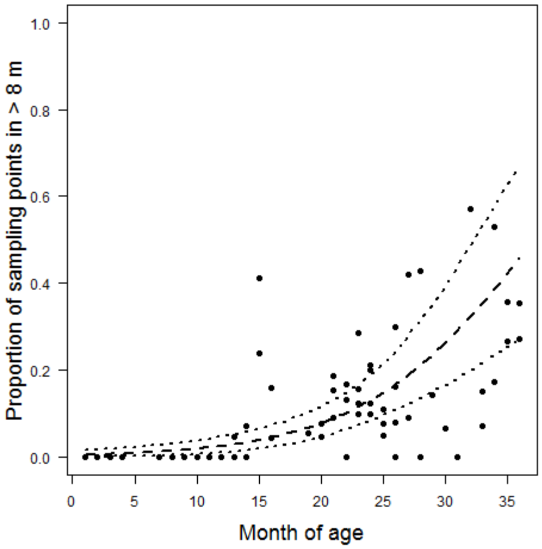

Figure 5. Proportion of sampling points in <8 m. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

To examine the amount of responsibility that each of the members of the dyad had in their proximity patterns, a Proximity Index was applied. It was calculated as the percentage of approach episodes made by the infant, minus the percentage of leave episodes made by the infant (Simpson, Simpson, & Howe, 1986). The formula was:

$$\left(\frac{Approaches\ by\ infant}{Approaches\ by\ mother + Approaches\ by\ infant} - \frac{Leaves\ by\ infant}{Leaves\ by\ mother + Leaves\ by\ infant}\right)$$

Proximity appears to depend mostly on the infant, but the infant’s role in maintaining proximity increased with age (estimate ± SE=0.072±0.029, X^2=4.838, *gl*=1, *p*=.027, Figure 6). The component measures of maintaining proximity did not change significantly over time: approaches (estimate ± SE=0.332±0.264, X^2=1.104, *gl*=1, *p*=.293) and leaves (estimate ± SE=-0.365±0.181, X^2=2.495, *gl*=1, *p*=.114). However, raw data show that leaves made by the infant increased with age (see Figure 7), whereas approaches did not (Figure 8).

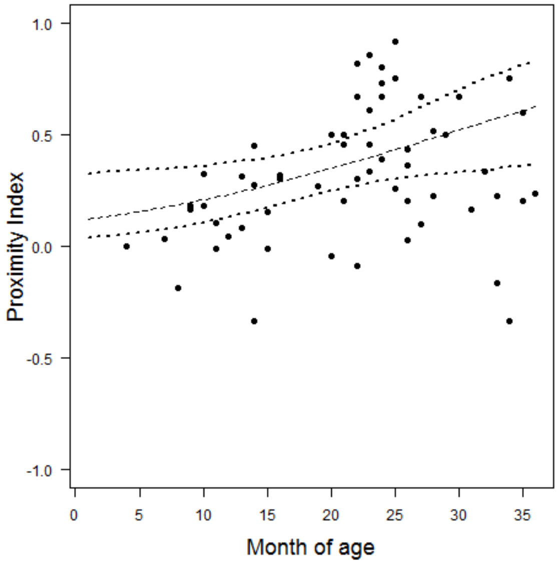

Figure 6. Proximity index. Given the presented formula, positive values mean that the infant was the main responsible of its proximity with its mother and with increasing values this responsibility would be greater. The opposite trend (negative values) implied that the proximity between the members of the dyad depend more on the mother, effect that would be greater with lowest values. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

In all models the effect of age was stable. Variation due to random effects was small and normal in all models except with regard to the slope of age within subjects in the models fitted for the proportions of time (ventro-ventral contact, gross body contact and proximity; Table 6). The residuals of the Gaussian models followed a normal distribution and the binomial and Poisson models showed dispersion values around 1.

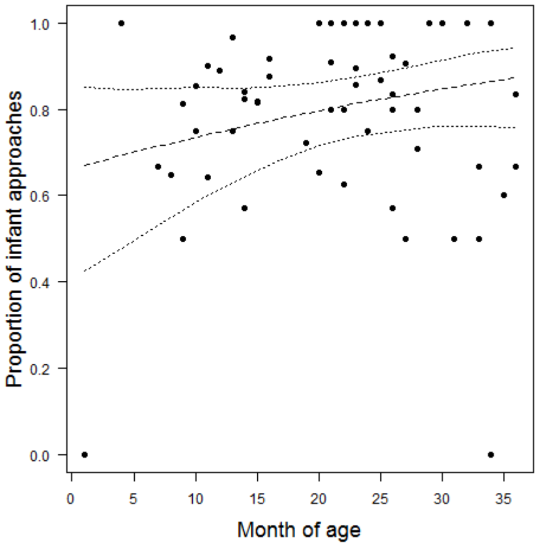

Figure 7. Proportion of infant approaches. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

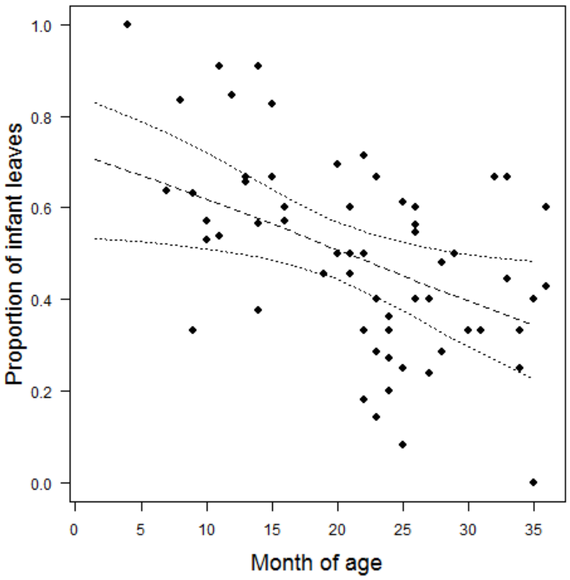

Figure 8. Proportion of infant leaves. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

Table 6. *Variation due to random effects in all models related to proximity and contact.*

Random effect	**Term**	**Focal data**					
		Ventro-ventral contact	**General contact**	**Proximity time**	**Approaches**	**Leaves**	**Proximity index**
Subject	Intercept	0.000	0.000	0.000	0.000	0.313	0.000
Subject	Age	0.946	1.010	0.984	0.000	0.000	0.000
Mother	Intercept	0.000	0.000	0.000	0.514	0.000	0.050
Random effect	**Term**	**Sampling points before and after focal observations**		**Scan data**			
		Points in proximity	**Points in >8**	**Points in proximity**	**Points in >8**		
Subject	Intercept	0.000	0.572	0.000	0.618		
Subject	Age	1.189	0.000	0.867	0.000		
Mother	Intercept	0.000	0.000	0.000	0.000		

Travelling Strategies

The first travel strategy for mothers of the two newborns was to carry their infants ventrally (almost 100% of the time). The change between ventral and dorsal carry was gradual and it was difficult to establish a specific moment of change. However, dorsal carry was first registered in focal observations at 8 days of age in one subject and at 31 days in the other. In the second month of age infants were carried dorsally by mothers, clinging to their backs to travel, but ventral carry was still the main travelling strategy (present in more than 60% of travelling time for both infants). Finally, in the third month of life dorsal carry became the most probable way of travel (corresponding to 74% of travelling time in the infant that reached this age during data collection), although ventral carry was the alternative strategy. Ventral carry was also present in the fourth month of age of the older newborn, but almost none travelling time was sampled in this month. Apart from the two newborns, ventral carry was also seen in the next younger infants but for periods of less than 1 min while feeding and lower than 30 sec while travelling.

Age also had a positive effect on the proportion of time in locomotion while travelling (estimate ± SE=2.923±0.469, X^2=10.397, *gl*=1, *p*=.001; Figure 9). The two infants that were carried by their mothers at the beginning of the study started to travel by themselves for brief moments at 9-10 months, but there were differences between subjects, in general, carrying was the main travelling strategy until their 14 months. The first periods of locomotion were alternated by longer periods of dorsal carry.

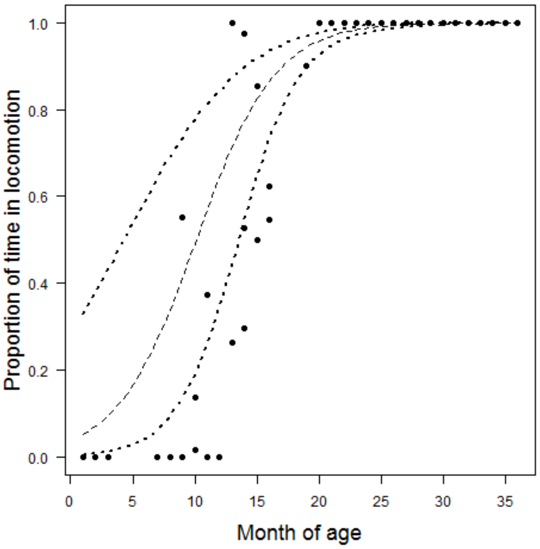

Figure 9. Proportion of time in locomotion while moving. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

The last events of dorsal carry occurred at 19 months in the subjects that achieved travelling independence during the study, but at this stage dorsal carry was mainly used in long travels or as a way to help the infants to cross difficult gaps between trees. A nonlinear effect of age on the rate of bridges was found (estimate ± SE=-0.940±0.549, X^2=15.855, *gl*=1, *p*=.000; Figure 10), with a peak approximately at this stage. However, bridges seem to start approximately at the first year of age and to finish at the second year of age (Table 7). Eight cases of external bridges were recorded during data collection; six were made by juvenile sisters, one by another infant male and one by an adult female (the grandmother).

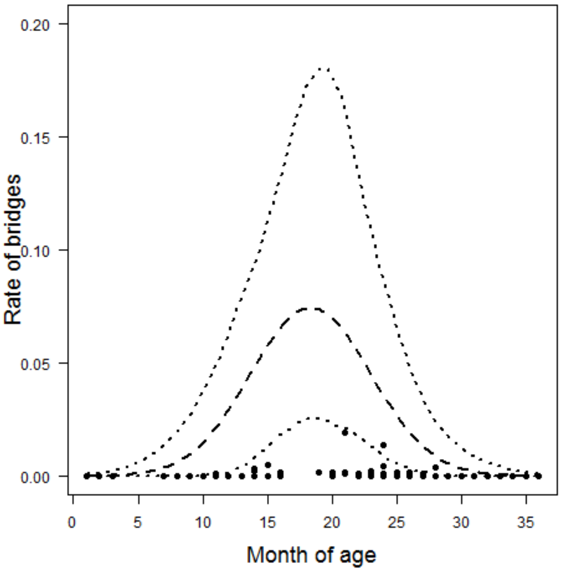

Figure 10. Rate of bridges while travelling. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

Table 7. *Month of age at first and last bridge for each subject (taken from focal samples and adlibitum data).*

Subject	**Range of age while data collection**	**Month of age of the first bridge**	**Month of age of the last bridge**
Valentín	7 to 14 months	11	14
Morita	9 to 16 months	11	16
Xtabai	13 to 19 months	15	19
Estrella	19 to 26 months	19	26
Panty	19 to 26 months	19	23
Francis	21 to 28 months	22	27
Nacho	22 to 29 months	23	29

The residuals of the model fitted for the proportion of time in locomotion were normally distributed and dispersion parameter of the model fitted for the rate of bridges was around 1. Also, the variation due to random effects was not high in the bridges model and a bit large in the locomotion model, mainly the one caused by the slope of age within subjects (Table 8). Random effects had a normal distribution in both models with the exception of the slope of age within subjects in the model fitted for the rate of bridges.

Table 8. *Variation due to random effects in all models related to travelling strategies.*

Random effect	Term	Proportion of time in locomotion	Rate of bridges
Subject	Intercept	0.172	0.563
Subject	Age	1.478	0.000
Mother	Intercept	0.000	0.000

Infant Behavioral Development

Exploration time increased with age (estimate ± SE=0.076±0.013, X^2=15.349, *gl*=1, *p*=.000; Figure 11)**.** Newborns did not present this behavior and I did not observe it in the next younger subject of the study when he was 7 months old. The first time I observed this infant exploring its environment at more than 1 arm reach and ingesting solid food was at 8 months of age, but in general subjects younger than 1 year explore less than 20% of the time, while the oldest subjects reach exploration times of 40%.

I also found that age had a positive effect on the proportion of time infants spent in social proximity (estimate ± SE=0.392±0.166, X^2=4.164, *gl*=1, *p*=.041; Figure 12) and social play (estimate ± SE=-0.823±0.129, X^2=19.928, *gl*=1, *p*=.000; Figure 13), but not in social contact (estimate ± SE=-0.199±0.117, X^2=2.179, *gl*=1, *p*=.139; Figure 14). Newborn infants were not observed in social play or social proximity with other group members. Social proximity was rare until infants were approximately 20 months and social play was rare during the first year of life. However, age had a nonlinear effect on social play, with a peak at 21 months. Finally, the proportion of time in social contact was rare and never greater than 11%.

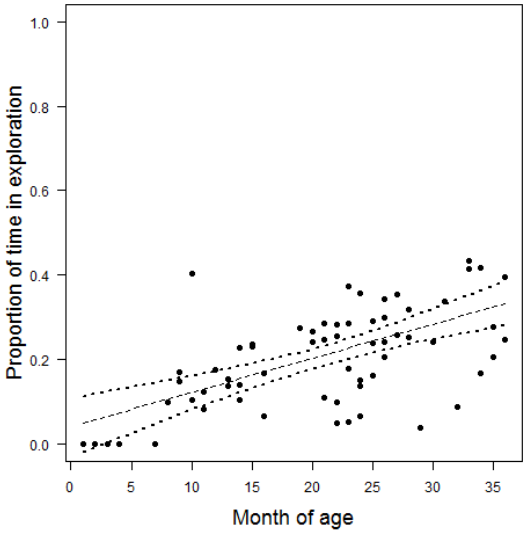

Figure 11. Proportion of time in exploration. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

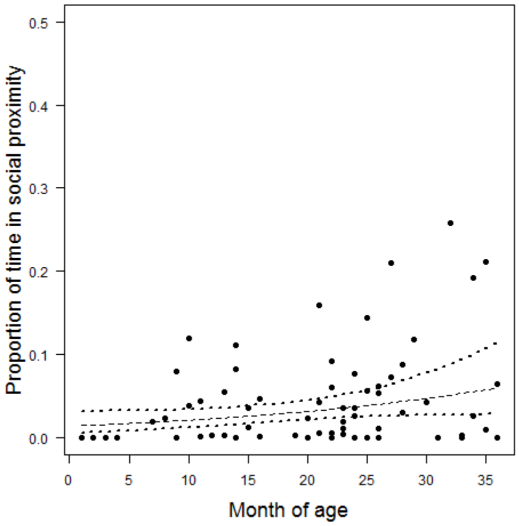

Figure 12. Proportion of time in social proximity. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

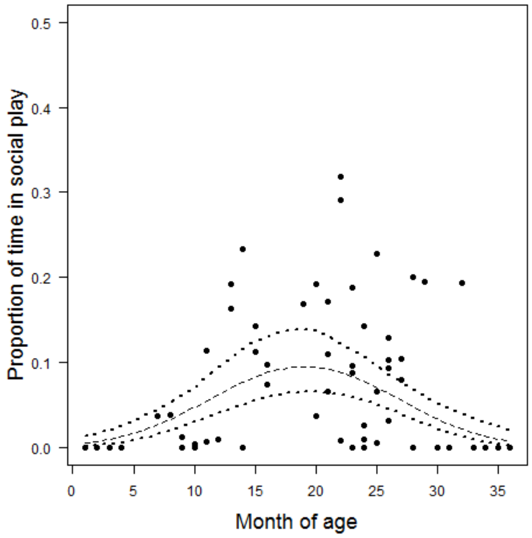

Figure 13. Proportion of time in social play. Dots represent raw data and the dashed line represents predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131). Dotted lines correspond to upper and lower confidence intervals.

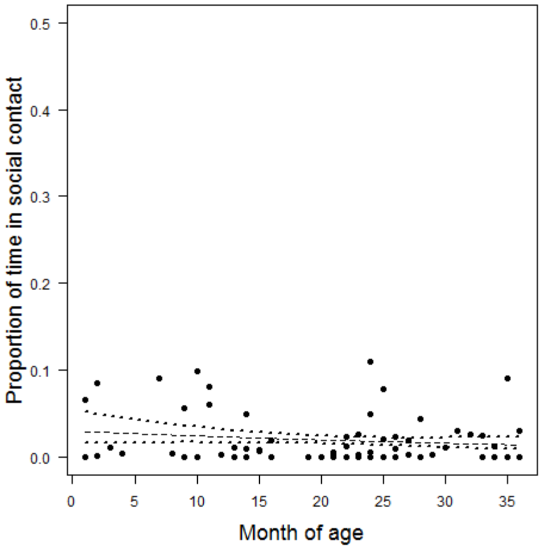

Figure 14. Proportion of time in social contact. Dots represent raw data and the dashed line corresponds to predicted values for age, with sex centered and group tenure at 0 given it was z transformed (the original mean of this variable was 12.615 and its original standard deviation was 8.131).

The residual distribution of these models fitted was normal, except for the model fitted for social contact. The effect of age was stable and the variation due to random effects was normal and little for all models (Table 9).

Table 9. *Variation due to random effects in all models related to social responses.*

Random effect	Term	Exploration	Social proximity	Social contact	Social play
Subject	Intercept	0.000	0.416	0.000	0.000
Subject	Age	0.022	0.000	0.171	0.000
Mother	Intercept	0.000	0.000	0.000	0.000

Rare Events

Episodes of aggression by other group members different than the mother toward infants were registered eight times during focal observations. Three were directed toward male infants from adult males (at 34 and 27 months of age), and five toward female infants: two from a juvenile sister (at 27 months of age), one from a juvenile female which was the aunt (at 20 month of ages) and two from an infant male (at 21 months of age).

Grappling was seen twice during the focal observations, both times by infant males. In one case an infant male of 28 months of age was resting at more than 8 m from his feeding mother. Approximately one minute after the beginning of the focal, the infant approached and made contact with a juvenile male, and a few seconds later grappling started, and last until the end of the focal. In the second case, a male infant of 35 months was also resting more than 8 m away his resting mother. A juvenile female approached and made a grooming solicitation to the infant, which was ignored. Twenty sec later she started to groom him for about 1 min, then stayed in contact with him for 2 ½ min and restarted grooming for a few seconds. After this, they remained in contact for about 2 min more, when they started grappling for about 1 ½ min. Later this same day, the infant started grappling with a subadult male out of focal observation time.

Discussion

In the next pages I summarize the results of my thesis and describe the developmental changes identified in the mother-infant relationship of this species throughout the first 3 years of life of the infant, going from a complete dependency period at the beginning of life through a progressive increase in infant independence. Then, I show that this process is very prolonged and soft in spider monkeys compare to other primate species of similar size and ponder different hypothesis that may explain this. I conclude with some remarks about the scope of my research and the need for more longitudinal data to be able to understand this phenomenon.

Mother-Infant Relationships Throughout the First 3 Years of Life of *Ateles geoffroyi*

As expected, mother-infant relationships changed with infant age. The newborns of the study were nearly always in contact and proximity with their mothers. With increasing age, infants remained less time in proximity with their mothers and often at more than 8 m from them. This was accompanied by a gradual increase in exploration time. Even though proximity usually depended on the infant during the first 3 years of age, this responsibility increased with time. Age also had a significant effect on the travelling strategies used by mothers and infants. Younger infants were always carried and a gradual increased in independent locomotion with a ceiling effect at 20 months was observed. Also, in the transition between infant carry and independent locomotion, bridges started to be used and a peak of this behavior occurred when carrying disappeared. As infants aged, they spent progressively more time in social proximity and social play, but the time in social play reached a peak at about 20 months, after which this behavior decreased.

The newborns of the study were nearly 80% of the time in ventro-ventral contact in the first month of age, but this percentage dropped to almost 50% in the third month of age of the older newborn. After this point, the proportion of time in ventro-ventral contact was drastically reduced with proportions of time between 0 and 0.2. However, this information needs to be further investigated given that the data for 4 months of age was taken from one subject and taking into account that no data was available from subjects of 5 and 6 months of age. Also, age did not had a statistically significant effect on this variable, which could be due to the dearth of data.

Gross body contact gradually decreased from birth to the first year of age and after this point mother-infant contact was almost only present when ventro-ventral contact or grooming occurred. The newborns of the study were almost all the time in contact with their mothers until the end of data collection. They started to break contact with their mothers at the beginning of their third month of age and leaved them for first time at the end of this same month. However, this data is derived from only two subjects and more evidence is needed to have more reliable information. Eisenberg (1976) reported similar results with a captivity population of *A. fusciceps*, in which infants showed the first cases of infant leaves approximately at their 10 weeks of age.

The distance between spider monkey mothers and infants seemed to increase with age. A decrement of the proportion of time in proximity was observed at about the first year of age. Infants also started to be at more than 8 m from their mothers a little before this age. At 3 years infants were never more than 40% of the time in proximity with their mothers and almost half of the time at more than 8 m from their mothers. Vick (2008) also found decreasing distances between mothers and infants with increasing age.

Infants started to show some signs of independence at 6 months of age when they began to frequently break contact and leave their mothers to explore the nearest environment. The first cases of exploration at more than one arm reach from the mother were observed at 8 months old. Even less information is available about infant feeding behavior on solid foods in spider monkeys. From my data it seems to start around the same time as exploration (8 months). This is congruent with the study of Eisenberg (1976), in which captive infants of *A. fusciceps* start to eat solid food at 8 months. Correspondingly, van Roosmalen (1980) observed that infants of wild *A. paniscus* start to eat solid foods after 6 months of age.

Infants were carried by their mothers their first months of life while travelling or feeding. Even dorsal carry was seen from the first month of age of the two newborns (with varying days of age); ventral carry was the most common travelling strategy until the third month. Eisenberg and Kuehn (1966) suggested ventral carry is present in black-handed spider monkeys until 4 or 5 months of age. Given the lack of data for infants of 5 and 6 months, it is hard to provide reliable data about the end of ventral carry from this study. However, available data suggest that this is very similar in wild *Ateles geoffroyi*. First, ventral carry was still present at the 4 months of age of the older newborn. Also, even though some cases of ventral carry were seen in the next younger infant of the study until he was 13 months old, these episodes lasted just a few seconds and mostly occurred when the infant was in ventro-ventral contact and the mother started to move. No other case of ventral carry was seen in any other subject, not even in the female infant that had similar ages (from 9 to 16 months).

During the second semester of life the first attempts of independent locomotion were observed (at 9 and 10 months of age of subjects), but dorsal carry remained the main travelling strategy until 15 months of age and totally disappeared by 20 months of age. This was consistent with the rate of bridges, which showed a peak at approximately 19 months, exactly when carrying stopped. These trends are not very different from what other field and captivity studies in this genus have suggested. Eisenberg and Kuehn (1966) reported carrying until the 1½ year of captive infants of *A. geoffroyi*. In wild spider monkeys van Roosmalen (1985) observed carrying until 12-15 months of age of *A. paniscus* and Symington (1987) found that carrying length varies within sexes in *A. belzebuth*, lasting in males 20.7 months and in females 17.3 months. Additionally, van Roosmalen (1980) observed that wild *A. paniscus* can still be carried until their 24 months when fatigued or during aggressive episodes, and usually used maternal bridges to cross gaps in the canopy at this age. Even though this was not the case in my study with regard to infant carry, the mother-infant dyads of OMYK used bridging until the second year of age.

Reject also started at 19 months of age and exploration reached proportions of time of more than 20% at this age. This could be a good indicator of independent feeding, given that between the first and the second years of age the body of spider monkeys seems to grow significantly (Eisenberg, 1976). However, it was not possible to determine a specific age of weaning from the data taken. Instead of ventro-ventral contact, nipple contact has been usually used to infer suckling (e.g., Fletcher, 1971). However, many times in this study it was not easy to distinguish between these two behaviors given the body position of the infant, whose head sometimes interrupted the view of the observer, and also due to the height in which spider monkeys tend to be, which does not allowed accuracy in detailed observation. Thus, nipple contact was seen only a few times in my study and statistical analysis could not be performed. Even if this was not the case, it is not possible to know if an infant is nursing when it has its mouth in the nipple of its mother (Cameron, 1998). Furthermore, it has been demonstrated that infants remained in nipple contact more time than is nutritionally needed (Brown & Pieper, 1973). Thus, accurate weaning ages are difficult to establish, but from the results of my research some inferences can be made taking into account reject episodes, ventro-ventral contact and the few registered cases of nipple contact.

Vick (2008) proposed varying weaning ages for this population ranging from 24 to 31 months, but the infants of my study seem to have later weaning periods. Nipple contact was even seen in subjects of 34 and 38 months. All infants except two were seen in ventro-ventral contact until the end of the study, even in one infant that reached an age of 38 months at the end of data collection. The oldest infant of the study (34 months old at the beginning of data collection) was never seen in ventro-ventral contact with its mother during focal observations or at sampling points. This could be related to its mother’s pregnancy, as she gave birth 4 months after the beginning of data collection. Also, the earliest case of nursing reject was seeing at 19 months old, while Vick (2008) saw the first rejections at 14 months old in the same population.

Weaning is a variable process within the members of a given species (Nicolson, 1987), thus the differences between my study and Vick (2008) are likely attributable to individual differences in maternal styles. For Geoffroy’s spider monkeys maternal rejection starts after the first year of age and nursing remains present at least until the third year of age. Vick (2008) mentioned an example of a female that still let her son of 31 months nurse, even though when she was apparently pregnant. In other *Ateles* species weaning also seems to occur very late. Eisenberg (1976) found evidence of the first weaning attempts in captive *A. fusciceps* at 14 months and intermittent suckling until 18 months of age. van Roosmalen

(1985) reported weaning of wild *A. paniscus* infants at the end of year 3, but also observed some cases of nursing in infants older than this age. Klein (1972) reported weaning between 2 and 3 years of age in wild *A. belzebuth,* and also in the wild Symington (1987) observed the first rejections in this species at 28.4 months for males and at 24.7 months for females.

The spider monkey mothers of my study did not showed any indication of maternal control. Except for a handful of data points, infants were responsible for the proximity between themselves and their mothers, and this responsibility increased with age. Specifically, infant leaves decreased throughout development and mother leaves increased. This could be due to the fact that rejection started, so while the mothers tried to reduce the infant opportunities to access the nipple, infants tried to increase their chances. However, because of the limited data, it was not possible to analyze the responsibility of the contact between mothers and infants, which would be very important to obtain a deeper understanding of the role that each member has in maintaining contact.

Only a few cases of retrieval and restriction were observed within the first year of infant life, principally when they start to break contact and leave their mothers (at 3-4 months of age). However, I believe that in the few months after this stage, these behaviors should significantly increase, but given data collection ended at this point I do not know what happens between the fourth month of age and the seventh month of age. After this point, retrieval was only seen in one dyad and in an unusual situation: ground play. This kind of play has been reported previously by some authors, and constitutes one of the four activities identified in spider monkeys when they go down the ground (Aureli et al., 2006). Ground play can be characterized as a type of social play that involves chasing in the ground and in which mainly juveniles participate (although I have observed adults taking part in the game). However, as in any other form of ground activity realized by spider monkeys, it represents a risk. Actually, when this activity takes place some adult sentinels often go down the ground and adopt a vigilance role (personal observation). The retrieval cases observed during ground play occurred by a mother whose son of 13 months was starting to participate in ground play. This infant was still dependent on his mother for travelling and he did not yet have well-developed motor skills, thus attempts and actual retrievals by the mother are not surprising in the context of ground play by young infants.

Social proximity showed a temporal increase around 10 months of age and later a gradual and steady increase at 20 months of age. This is similar to what Vick (2008) reported: an initial increment in social interactions after the first year of age and a next one about 2 years of age. Social play also started to be progressively more present in the subjects of the study around 10 months of age and reached a peak at 21 months of age. Infants around this age spent approximately 30% of their time in this activity. After this point the proportion of time in social play decreased. From the data of this study, older subjects seem to rarely play with other members of the group. Finally, social contact did not change significantly with age and remained with proportions of time lower than 0.1 along the 3 years of age.

Thus, the changes in mother-infant interactions and infant behavior suggest two critical periods of independence. The first one occurs around the first year of age and is characterized by the beginning of independent locomotion and exploration, a significant increase in mother-infant distance, and an initial increment in the proportion of time infants spent in social interactions. A second and more drastic transition happens around 20 months of age and is identifiable by the start of rejection, the end of carrying and a second increase in the time infants spent in social activities.

Infant Development of Spider Monkeys Compared to Other Species

Some reproductive indicators suggest that the behavioral development of infant spider monkeys is very slow compared to other primates of similar size (see Appendix). Thus, I expected a prolonged period of infant dependence and a delay behavioral development in *Ateles geoffroyi* compared to what has been reported for other primate species. Although little information exists to support a slow developmental trajectory (Vick, 2008), the data presented above seem to confirm this.

First, spider monkey infants seem to spend more time in contact with their mothers compared to other species. Whereas in the first month of age, free-ranging infant macaques spend no more than 80% of the time with their mothers and less than 40% in their fourth month of age (Berman, 1978), the newborns of my study were almost always in contact with their mothers until the end of data collection (at 2 and 4 months old). Even compared with wild long-tailed macaques (*Macaca fascicularis*) and howler monkeys, which mothers are almost 100% percent of the time in contact with their infants in their first month of life, the difference is quite important, given that at 4 months infant long-tailed macaques spend less than 30% of the time in contact with their mothers and infant howler monkeys less than 80% of the time (Karssemeijer, Vos, & Hooff, 1990; Pavé, 2016).

Second, the difference between spider monkeys and other similarly sized monkeys species was marked with regard to the time infants spent in proximity with their mothers. While mother-infant dyads of wild olive baboons are usually less than 80% of their time in proximity during the fourth month of age and less than 50% at the end of their first year (Nash, 1978), the dyads of my study were almost 100% of the time in proximity during the first 4 months of life of infants, and, except in one data point, more than 70% of the time until their first year of life. The contrast is even sharper with rhesus macaque infants, which remain in proximity with their mothers less than 40% of the time in their fourth month of age and less than 20% of the time in proximity by 7 months of age (Berman, 1980).

Third, in contrast to what has been reported with rhesus macaques (Hinde & Spencer-Booth, 1971), but similar to howler monkeys (Pavé et al., 2015), the infants of my study were the ones that break contact and leave their mothers for first time and in these initial events mothers frequently reestablished contact or proximity. Furthermore, they did not show indicators of stress during their first separations compared to macaques (Maestripieri, 1994b, 1995). Additionally, the first time the infants of my study broke contact and separated from their mothers at a distance of more than one arm’s reach was very late compared to what has been described for other monkey species (see Appendix).

Differences with regard to carrying are also evident. While the mothers of this study carried their infants until 19 months of age, howler monkey (*Alouatta caraya)* mothers stop carrying at 7 months of age (Pavé et al., 2010). Olive baboons and Yunnan snubnosed monkeys (*Rhinopithecus bieti*) carry their infants until 17 months of age (Nash, 1978) and

12 months of age (Li et al., 2013), respectively, despite being much heavier than spider monkeys (see Appendix).

Additionally, the start of rejection reported here and by Vick (2008) is very late compared to primate species of similar size such as rhesus macaques or howler monkeys, which start to reject their infants from the first month of age (Hinde & Spencer-Booth, 1967; Pavé et al., 2010). The low rates of rejection in my study were also a remarkable result (see also the data of Rodrigues, 2007), as the way in which mothers rejected their infants, which usually just involved avoiding the infant, contrary to what has been reported for other species (e.g., Maestripieri & Carroll, 2000). Macaque mothers often bite or slap their infants, and some more rough forms of aggression from mother to infant have been observed (Troisi & D'Amato, 1983). In contrast, only eight cases of aggression from mothers to infants were observed during the focal observations of my study, none of them involving more than facial threats, short chases, soft bites or light slaps.

Finally, the social behavior of the infants in my study appear to be delayed compared to other species. Social play was not observed in the newborn infants of the study but was already present in the next younger infants of the study (of 7 and 9 months old). In other species social play begins earlier. For example, *Rhinopithecus bieti* infants began to play with others at 81 days (Li et al., 2013) and rhesus monkeys at 21-28 days (Hinde, Bowell, & Spencer-Booth., 1964). The peak in social play has also been reported in other primate species, albeit earlier (e.g., at around 6 - 7 months in baboons, Nash, 1978).

Thus, although direct comparative research would be needed to be able to make reliable comparisons between spider monkeys and other species, *Ateles geoffroyi* mothers seem to invest in their infants for a longer time. Additionally, even though more research is needed to be able to define the maternal style of this species, the few maternal rejections and aggressive behaviors toward the infants of my study, and its benign quality, strongly suggest that *Ateles geoffroyi* mothers are very tolerant toward their infants.

Accounting for Slow Life Histories

The results of my present study confirm that dependency from infant to mother lasts very long in *Ateles geoffroyi* compared to what has been reported for other primate species of similar or even greater size (see Appendix). Different types of explanations have been proposed to understand the variation among species with regard to their life histories (Godfrey, Samonds, Jungers, & Sutherland, 2001; Pereira, 2002). The design constraint or allometric hypothesis suggests that the length of variables associated with life history correlates with the body size of species (Pereira, 2002; Taylor, 1965; Western, 1979). Thus, it predicts that species with large bodies tend to have slow life histories (Purvis, Webster, Agapow, Jones, & Isaac, 2003), in terms of gestation length, life-span, age of maturity, neonatal size, interbirth interval and age at weaning (Calder, 1984; Harvey, Martin, & Clutton-Brock., 1987). However, taking into account that species of similar or greater body size than spider monkeys show faster juvenile periods (see Appendix), the extended life history of spider monkeys could not be explained by this hypothesis.

An alternative allometric explanation that suites better with the longer life-span of spider monkeys is that the size of the brain is what determines the life histories of each species (Sacher, 1959; Sol, 2009). This could be explained by the fact that large brains favor survival and long life-spans because of a *cognitive buffer* that allows organisms to develop better strategies to face environmental unpredictability (Allman, McLaughlin, & Hakeem, 1993; González-Lagos, Sol, & Reader, 2010). Relationships found between life-span and brain size support this idea (Sol, 2009). An alternative explanation is that large brains need more time to develop, so maternal investment during prenatal and postnatal life is increase to promote the growth of large brains, which in turn causes slow and long life-histories (Barrickman, Bastian, Isler, & van Schaik, 2008; Barton & Capellini, 2011; Isler & van Schaik, 2009).

A causal relationship between the relative size of the brain and the variation in some ecological variables has been also proposed (Barton, 1996; Clutton-Brock & Harvey, 1980; DeCasien, Williams, & Higham, 2017). Frugivorous and omnivorous species tend to have relative larger brains than folivorous species (Harvey & Bennett, 1983; Milton, 1981), and frugivorous primates usually have longer and slower life histories (Leigh, 1994; Wich et al., 2007). Different causal relationships between these variables have been analyzed. Some have suggested that the nutritional components of frugivorous diets favor larger brains (Zink & Lieberman, 2016). Conversely, others emphasize that large brains demand great amounts of energy, requiring highly energetic diets (Holliday, 1986). Related to this, it has been proposed that given the high cost for developing larger brains, less energy is leftover to the growth of other body parts, so the size of the gut was reduced by an easily digestible diet (Aiello & Wheeler, 1995). This would apparently apply to spider monkeys, given their fast gut passage times in relation to their body size (Milton, 1981, 1984; Lambert, 1998). However, new evidence suggests that the relationship between brain size and gut size is not valid (Navarrete, van Schaik, & Isler, 2011).

Fruit maturity patterns can be highly unpredictable and the availability of fruits sometimes can be very scarce (Wright, Carrasco, Calderon, & Paton, 1999), thus a different type of explanation for the larger brain size of frugivorous species is that high quality diets require that animals have high cognitive abilities to find food resources (Martin, 1996; Milton 1988), such as spatial information storage and retrieval (Clutton-Brock & Harvey, 1980) and extracting foraging skills (Gibson, 1986). This makes sense given that the relative size of the brain seems to vary according to the cognitive skills of each species (Chittka & Niven, 2009; Deaner, Isler, Burkart, & van Schaik, 2007).

Spider monkeys are characterized by consuming ripe fruits that are found within large and widely dispersed patches (Di Fiore &Campbell, 2007; Di Fiore, Link, & Dew, 2008; van Roosmalen & Klein, 1988; Wallace, 2005). Some have suggested that they preferred fruits with high content in easily digested carbohydrates and/or lipids (Di Fiore, Link, & Dew, 2008), but a recently research by Stevenson and Link (2010) showed evidence that spider monkeys (specifically, *Ateles belzebuth*) have a generalized type of diet. Any case, they need to be able to select, from randomly dispersed food resources in time and space (van Roosmalen, 1985; Symington, 1988b; Dew, 2005; Wallace, 2005; Di Fiore & Campbell, 2007). Thus, evidence of seasonality variation in ranging patterns and habitat use has been found, which seems to correlate with monthly fruit production (Wallace, 2006). Also, when ripe fruit is scarce, spider monkeys seem to remain in small areas and eat alternative food sources (Felton et al., 2009; Schaffner, Rebecchini, Ramos-Fernandez, Vick, & Aureli, 2012; Wallace, 2006), which have been interpreted as a way to maximize energetic intake (Suarez, 2006). Thus, spider monkeys are flexible in the type of fruits they eat and in the overall food items they use and seem to adjust well to environmental challenges (Di Fiore, Link, & Dew, 2008; Schaffner et al., 2012). Additionally, as other species characterized by high degrees of fission-fusion dynamics, spider monkeys adjust their sub-group sizes according to food availability to reduce feeding competition (Kummer 1971; Chapman, Wranghman, & Chapman, 1995), and to do so, a key component is an advanced communication system (Ramos-Fernández, 2008). Fruit selection also seems to require coordination between the olfactory and visual systems (Hiramatsu et al., 2009).

This selective, adaptable and flexible process suggests that the *Ateles* genera use complex cognitive skills to obtain their food resources, which may account for enlarged brain size, as proposed by the cognitive buffer hypothesis. In general, the process of acquiring the knowledge and skills needed to exploit variable food source in type, availability and space, is strongly related to social learning (Kaplan, Hill, Lancaster, & Hurtado, 2000; Street, Navarrete, Reader, & Lalland, 2017; van Schaik & Burkart, 2011; Navarrete, Reader, Street, Whalen, & Laland, 2016). However, with a group of reintroduced immature spider monkeys, Milton (1981) found evidence that suggests that in *Ateles* feeding skills such as distinguishing ripe or high quality fruit are acquired by trial and error and/or are inherited. These individuals were never exposed to the behavior of adult spider monkeys, so no opportunity of social learning could exist. Still, through comparative analysis between different populations of *Ateles geoffroyi*, evidence of social learning related to feeding strategies has been found (Santorelli, Schaffner, & Aureli, 2011; Santorelli et al., 2011).

Also, researchers have found social behaviors and behaviors of other domains that can be classified as traditions in spider monkeys (Santorelli, Schaffner, & Aureli, 2011; Santorelli et al., 2011). Social learning has also been interpreted an indicator of large brain sizes and longer life-spans (Kaplan et al., 2000; Street et al., 2017). It increases with group size (Henrich, 2004), and in turn group size correlates with neocortex size (Dunbar, 1992, 2003). The explanation for this is that with increasing group size the cognitive challenges are bigger (Byrne, 1996), so tools as social learning are needed, and thus an increase in brain size is demanded (Street et al., 2017). This relation between social and cognitive complexity and the size of the social brain was defended by the *social brain hypothesis* (Dunbar, 1998). Although social complexity has been usually defined according to group size (e.g., Dunbar, 2003), in a recent review, it was mainly defined as the number of differentiated relationships between the members of the group (Berman & Beehner, 2015)

The above explanation might also apply to spider monkeys, which live in groups with high degrees of fission-fusion dynamics and with clearly differentiated sex-specific social roles (Vick, 2008). The high degree of fission-fusion dynamics of spider monkeys has been classified as a complex characteristic of social organization and a highly demanding social system with respect to complex cognitive abilities (Aureli et al., 2008; Milton, 2000; Barrett, Henzi, & Dunbar, 2003). Thus, several factors may select for complex cognitive abilities in spider monkeys and, in turn, a slow developmental trajectory to afford ample learning time.

An alternative explanation proffered to account for the slow developmental trajectory in spider monkeys is their near exclusive reliance on arboreality (Ross & Jones, 1999). It has been proposed that in arboreal species contact could be very advantageous to prevent the risk of infants falling out the tree (Chalmers, 1973). The risk of injury or death from a falling infant would be high for arboreal species, particularly those that use the upper canopy, which is the case in all spider monkey species (Di Fiore, Link, & Dew, 2008). This could also explain the extended carrying time seen in this study. For example, even though long-tail macaques are smaller than rhesus macaques (see Appendix); they spend more time in contact with their mothers (Berman, 1978; Karssemeijer et al., 1990)

However, a congener, *Alouatta* (howler monkeys) are also a strictly arboreal species, but have a much shorter developmental trajectory compared to spider monkeys, with females reaching puberty at as early as 3 years of age (Glander, 1980). Furthermore, the interbirth interval is much shorter than in spider monkeys - 19 to 22.5 months (Glander, 1980; Fedigan & Rose, 1995). Even mother-infant dyads of howler monkeys also spent high amounts of time in contact (at 4 months less than 80%; Pavé, 2016) compared to other species such as baboons (at 4 months less than 50%; Altmann, 1980) or macaques (at 4 months less than 50%; Berman, 1978), this times are still low compared with spider monkeys (at 4 months almost 100%). Also, howler monkeys start to move by themselves from the second month of age and stop being carried by their 8 months of age (Pavé, 2016); much earlier than what I found with spider monkeys. Thus, arboreality is unlikely to fully account for the slow developmental pace in spider monkeys. In this case, brain size seems to be a key component to explain their life-history differences, which could be related to their diet differences (Fedigan & Rose, 1995). While spider monkeys are a highly frugivorous species as explained before, howler monkeys do not eat regularly fruit and can be better described as a folivorous species (Di Fiore & Campbell, 2007).

High Maternal Tolerance and Low Infant Risk

Female spider monkeys appear to be very tolerant with their infants in the transition to independence. Thus mother-infant conflict seems to be less drastic in the *Ateles* genus compared to other primate species. A key aspect that determines maternal styles is the risk that ecological and social characteristics represent for the immature (Maestripieri, 1993, 2001). Basically, when infants experienced a higher risk, the mothers need to be more protective with them to increase their chance of survival, but also more rejecting to promote their independence and particularly the development of self-protection behaviors (Nicolson, 1987). Thus, below I evaluate the potential risk of the spider monkey infants to determine whether it corresponds to its low maternal rejection.

Maestripieri (1994a) made special emphasis on the quality of infant handling as a determinant feature of infant risk and suggested that it mostly depends on the quality of female-female relationships given that infant handling is mainly executed by adult females. The nature of the relationship between female spider monkeys has been classified as dispersal-egalitarian, which means that they do not form dominance relationships (Aureli & Schaffner, 2008; sensu Sterck et al., 1997). According to the related literature, this would explain the highly tolerant behavior of the mothers of this study (e.g., Li et al., 2013). However, spider monkeys do not seem to follow the pattern of infant handling supported by

Maestripieri (1994a). In a recent study, it was found that in wild Geoffroy's spider monkeys adult males are more involved in infant handling than adult females that are not the mothers (Evans, Pavelka, Hartwell, & Notman, 2012). In this sense, the relationship between adult males with adult females and their infants must be more relevant with regard to infant risk in this species.

It has been identified that male spider monkeys tend to be aggressive with females (Campbell, 2003) and present more chasing behavior than adult females, which is mostly directed toward adult females (Campbell, 2003; Fedigan & Baxter, 1984). However, aggression from males toward females seems to be of lower intensity than aggression between males (Link, Di Fiore, & Speher, unpublished data, cited by Shimooka et al., 2008). Also, some episodes of aggression have been reported toward juveniles (Chapman, Fedigan, Fedigan, & Chapman, 1989; Valero, Schaffner, Vick, Aureli, & Ramos-Fernández, 2006; Vick, 2008) and infants (Shimooka et al., 2008). Chapman, Fedigan, Fedigan, and Chapman (1989) found that intragroup aggression toward immature monkeys was identified as an important source of injury and death. Vick (2008) supported this for the immature population of OMYK. In total, eight cases of infanticide have been reported in this genus (Álvarez et al., 2015; Gibson et al., 2008; Shimooka et al., 2008; Vick, 2008), from six different populations, which represent four species of *Ateles*.

van Schaik and Janson (2000) suggested that spider monkeys should be prone to infanticide given their prolonged mating period, their polyandrous mating system and their slow development. This is supported by the fact that all cases of infanticide reported have been perpetrated by adult males and directed toward infant males. Conversely, Shimooka et al. (2008) proposed that this could be explained by an attempt to avoid the long interbirth intervals that follows from infant male births (Symington, 1987). The same kind of trend has been found in bonobos and chimpanzees (Wilson et al., 2014). Actually, Gibson et al. (2008) showed evidence that the interbirth intervals in spider monkeys were shortened to less than 1 year after infanticide.

However, infanticide is nonetheless rather rare in spider monkeys (Álvarez et al., 2015; Palombit, 2012), and it does not make much sense that adult male spider monkeys injured or attack immature males given that they are closely related to each other (Di Fiore, Link, Schmitt, & Spehar, 2009) and represent future coalition partners in intergroup encounters (Álvarez et al., 2015). Given that lethal aggression toward weaned juveniles has also been observed (Valero et al., 2006); an alternative explanation is that it represents a strategy to reduce male reproductive competition when within-group competition is higher than inter-group competition (Álvarez et al., 2015; Valero et al., 2006). This is consistent with the opposite reproduction alternative reported by Aureli et al. (2006), in which instead of killing relative immature males, adult males raid neighboring territories in an attempt to increase reproductive opportunities when female reproductive availability is scarce in their territory.

Even though in this study I only observed eight cases of aggression from other members of the group different than the mother toward the infants, infant spider monkeys do not seem to be safe with regard to their social environment and thus it would be predicted more rejecting and protecting maternal styles. However, the high degrees of fission-fusion dynamics of this species could make a big difference given that mothers can select their foraging groups and thus control the chances of infant aggression. Correspondingly, mothers usually travel in small subgroups or alone and stay far away the boundaries of their home ranges, which are interpreted as a protective maternal behavior (Chapman, 1990). In this sense, Aureli et al. (2008) suggested that one of the benefits to individuals for departing from subgroups is to "reduce infanticide risk by avoiding conspecifics during early lactation" (p. 648). While controlling their foraging partners, mothers also control the social density of the subgroups in which they and their infants are in. Thus, it is possible that spider monkey mothers are very tolerant with their infants given they are mostly alone with their infants or in groups with very low density.

Finally, as suggested by de Lathouwers and van Elsacker (2004) to explain the higher rate of reject behavior in bonobos and chimpanzees, it is possible that spider monkey mothers show high maternal investment and especially low maternal rejection, given their reduced social activity compared to other species (Aureli & Schaffner, 2008). For example, rhesus macaques live in cohesive groups composed by matrilineal societies in which females frequently participate in social interactions. Thus mother-infant interactions could hinder more probably other types of activities, which could trigger more often maternal rejection. The study made by Berman (1980) might support this idea. This researcher found that mothers of rhesus macaques that were part of a less well-establish matrilineal structure spent more time with their infants, reject them less and were more responsible for the proximity between them compared to mothers of a different population with longer matrilines.

This last explanation is in concordance with the timing hypothesis of mother-offspring conflict, which suggests that mothers start to reject their infants to prevent the interference of other mother activities because of nursing (Altmann, 1980; Dunbar & Dunbar 1988). Supporting this hypothesis, reject behaviors may occur primarily when mothers are feeding themselves (Li et al., 2013), however, this was not case in my study, in which maternal rejection was mainly present during resting. One possibility in that in these occasions the mother was interacting with others, but further studies would be needed to properly answer this question.

With regard to the ecological variables that could represent a risk for spider monkey infants, Bowlby (1969) suggested that predation was an important selective pressure to the evolution of mother-infant attachment. For example, evidence exists that in populations of rhesus macaques with greater predation risk mothers and infants spent more time in contact compare to safer populations (Johnson & Southwick, 1984). Also, Nicolson (1982) observed that baboon mothers carry their infants when escaping from a predator, even if the infant has already reached independent locomotion. Finally vervet monkey mothers were found to be more protective and vigilant with their infants in the context of predator alarms (Hauser, 1988).

In spider monkeys, it has been proposed that given their large body size, predation risk is not high (Wallace, 2008). However, six cases of predation from jaguars and pumas directed to adult members have been reported (Chinchilla, 1997; Emmons, 1987; Matsuda & Izawa, 2008). As noticed by Matsuda and Izawa (2008), given their smaller size, immature monkeys are more vulnerable to predation attacks from small carnivores and raptors. In addition, a case of predation by an eagle directed to an infant was reported by Julliot (1994). Thus, Shimooka et al. (2008) suggested that predation risk in this genus could be greater than we thought. Moreover taking into account that researchers have begun to discover that spider monkeys are not completely arboreal but use the ground for activities such as drinking water, eating, playing and escaping from attacks (Aureli et al., 2006; Campbell et al., 2005; Shimooka et al., 2008), which makes them more vulnerable than previously understood.

Even more research is needed to be able to define the predation risk of the species, it seems low compared to the one other primate species. For example, from 20 years of study, in OMYK only two cases of predation attacks toward spider monkeys have been witnessed (C. Schaffner, personal communication), compared with five cases observed during a 10 year study of a wild population of baboons (Cheney et al., 2004). These inter-species differences with regard to predation risk can be related to the fact that arboreal life reduces predation opportunities (Crook & Gartlan, 1966).

The lower predation risk compare to other species conforms to the relaxed maternal style of spider monkey, but the general risk of a population might be better inferred from the mortality rates of a given species. In OMYK mortality rates of 20% for males and 15% for females have been reported (G. Ramos-Fernandez, personal communication, cited by Shimooka et al., 2008). Also, 25.8% of infant males and 4.8% of infant females die within the first year in spider monkeys of La Macarena, Colombia (K. Izawa, A. Nishimura and Y. Shimooka et al., unpublished data, cited by Shimooka et al., 2008). However, the percent of deaths seem low when compared to 57% infant deaths reported in some populations of wild vervet monkeys (Caughley, 1966), the 38% of wild baboon infants that die before their first year of age (Cheney et al., 2004) and compared to the 50% of chimpanzee infants that die before weaning (Nishida et al., 2003).

Conclusions

Developmental studies are fundamental to understand the behavioral patterns of organisms. Approximately 70 years ago John Bowlby realized this and emphasized that the early relationship between the infant and the mother was a key to understand the behavioral development of subjects. This fundamental idea has influenced the work of human and non-human primate researchers since then. However, most of the studies have focused on only a few primate species (Pereira & Fairbanks, 2002; Vick, 2008). My thesis was an attempt to fill in part this knowledge gap and specifically to characterize mother-infant relationships in *Ateles geoffroyi*.

The results of my study begin to elucidate how mother-infant relationships change within the first years of the life of spider monkeys and confirm that this species is an interesting model for studying this phenomenon, which could lead to a better understanding of the inter-species differences with regard to mother-infant relationships. It appears that the relationship between mothers and infants in *Ateles geoffroyi* is characterized by a long dependency period and a delay in behavioral development compared to other primate species of similar and bigger size such as macaques, baboons and howler monkeys. My results were analyzed in the framework of different hypotheses proposed to explain slower life histories, from which the relative size of the brain may account for the differences observed between spider monkeys and other species. Variables such as body size and arboreal life of the genus were not enough to explain the slower developmental history of spider monkeys compare to other primates. Additionally, as suggested by the presented evidence, the high cognitive skills of spider monkeys in terms of feeding and social behavior could have an intricate relationship with their relative large brains.

My data also shows that spider monkey mothers have a highly tolerant maternal style during the transition toward infant independence in comparison with the patterns observed in other primate species of similar body size. Given that high rejecting maternal styles correlate with the risk experienced by the infant in a given species, I review the literature available with regard to some ecological and social characteristics of the species that could represent a risk for the infant. I conclude that although infant spider monkeys experience some risk, this is lower than what has been reported for other species. Also, I suggested that the high degrees of fission-fusion dynamics of the genus seem to allow mothers to reduce the social risk by selecting their temporal social partners. This could explain the low frequency and the benign nature of rejecting behaviors observed in the spider monkey mothers of my study.

It must be considered that the scope of these results is limited given the low number of mother-infant dyads and the short duration of the study. Thus, longer investigations with larger sample sizes would be needed to confirm the present results and to elucidate additional information about mother-infant relationships in spider monkeys. The importance of longitudinal research with this respect is essential to be able to do within subject analysis of mother-infant relationships. In this regard, the short duration of my data collection did not allowed me to make intrasubject analysis (e.g., some subjects had just two data points), which are highly important to see if the developmental patterns observed are present at least in the majority of subjects or correspond to a random product of the data collected from various subjects of different ages. Longitudinal analysis are even more relevant considering that we still do not have information on offspring between 4 and 7 months, given that in my study there no infants of that age during data collection. Also, investigations with more observation time are needed to be able to analyze important measures, which are relatively rare, that were not sufficient in number for data analysis in my study (e.g., body contact index). Additionally, this is very important given that the small sample size of this research could reduce the statistical power of the models and lead to type II error in some measures such as ventro-ventral contact (Randolph & Myers, 2013). In this regard, I believe it is important to consider alternative sampling techniques to achieve longer observation times (e.g., full day follows of mother-infant dyads).

More extended research is also important to analyze interspecific differences among mother-infant dyads within the species. Many factors such as maternal experience and infant sex affect the relationships between mothers and infants in other primate species (see Fairbanks, 1996), so I infer that this should also apply to *Ateles* species. For example, it is very likely that spider monkey mothers invest more in their sons compared to their daughters taking into account that in this genus males are largely the philopatric sex (Aureli et al., 2013). Moreover given the sex differences already found with regard to juvenile behavior (Rodrigues, 2007, 2014; Vick, 2008) and the apparent bias from adult males to attack weaned and unweaned males (Fedigan & Baxter, 1984).

The special quality of mother-infant relationship in this species suggests that the role of the mother as psychic organizer (Bowlby, 1951) could be even greater than in other species. Thus, once identified interspecific differences between mother-infant dyads in spider monkeys, its differential effects on the behavioral development of infants should be explored.

Additionally, dependency length seems to vary within *Ateles* species (van Roosmalen, 1985), more research about mother-infant relationships in spider monkeys is needed to study possible differences between species and between populations. For example, the amount of risk experienced by an infant can differ between species or specific populations as has been found for other genus (e.g., Maestripieri, 1994b). This can be inferred from the study of Shimooka et al. (2008), which suggested that *A. geoffroyi* have slightly more immature population (infants and juveniles) compared to other species of spider monkeys, which in turn suggests that in this species the infants have lower risk in relation to other *Ateles* species. Also, the low risk identified could be related to the population itself.

Finally, I want to conclude by making special emphasis in the importance of increasing conservational strategies taking into account the results of my study. In general, given that primates are altricial species (Nicolson, 1987); mothers and newborns are highly vulnerable with regard to aspects such as predation risk and intraspecific aggression. Also, during infant dependence mothers need more food resources to supply their energetic needs and the one of their infants, but in turn have to invest additional energy in carrying and nurturing their infants (Loudon & Racey, 1987). For arboreal and frugivorous species such as spider monkeys this highly costly process could be even more demanding when habitat fragmentation is high. This could be related with the fact that long-lived species that reach maturity at a relatively late age are in greater risk of extinction (Hutchings, Myers, García, Lucifora, & Kuparinen, 2012). In this sense, the slow developmental period of *A. geoffroyi* supported by the results of my study should promote conservational strategies to prevent the extinction of spider monkeys.

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Appendix

Table A1. *Comparative table of reproductive and developmental indicators of Ateles geoffroyi and other primate species of similar or greater body size.*

		Ateles geoffroyi	***Alouatta caraya***	***Rhinopithecus bieti***	***Papio anubis***	***Macaca mulatta***	***Pan troglodytes***
Weight(a)	♀	8,290 g	6,420 g (6,800 g)	20,333 g	23,750 g	11,000 g	42,700 g
	♂	7,250 g	4,330 g	12,600 g	13,050 g	8,800 g	33,700 g
Sexual maturity		4-5 y	3 y	5 y	4.5-5 y	41.9 ± 0.1 y	10.8 y
Gestation		226-232 d	187 ± 7 d	6.5–7 m	6 m	166.5 d	225.3 d
Interbirth interval		28-30 m	14–16 m	-	718-759 d	21 m	5.15 y
Out of contact		62 d	-	39 d	-	9 d	$3^{1/2}$-$5^{1/2}$ y
Out of one arm reach		89 d	-	81 d	-	13 d	-
First reject		19 m	1 m	2 m	6 m	1 y	-
Last carry		19 m	7 m	12 m	17 m	-	4-8 y
Source		1-6	7-9	10-11	12-13	14-18	19-21

Note: - = none available data found. b = all body weights were taken from Fleagle (2013). The sources of the information are the following: (1) this study; (2) Campbell and Gibson (2008); (3) Chapman & Chapman (1990); (4) Di Fiore and Campbell (2007); (5) Fedigan and Rose (1995); (6) Vick (2008); (7) Pavé et al. (2010), (8) Raguet & Pavé (2010); (9) Glander (1980); (10) Li et al. (2013); (11) Quan & Xie (2002); (12) Altmann, 1980; (13) Nash (1978); (14) Hinde & Spencer-Booth (1964); (15) Drickamer (1974); (16) Silk, Short, Roberts, and Kusnitz (1993); (17) Berman (1988); (18) Altmann, Altmann, Hausfater, and McCuskey (1977), (19) Nishida et al. (2003); (20) Wallis (1997); (21) van Lawick-Goodall (1967).