

## RESEARCH ARTICLE

How Do Demographic and Social Factors Influence Parent-Offspring Conflict? The Case of Wild Black and Gold Howler Monkeys (*Alouatta Caraya*)ROMINA PAVÉ<sup>1\*</sup>, MARTÍN M. KOWALEWSKI<sup>2</sup>, GABRIEL E. ZUNINO<sup>3</sup>, AND ALEJANDRO R. GIRAUDO<sup>1,2,3,4</sup><sup>1</sup>Instituto Nacional de Limnología (CONICET), Ciudad Universitaria, Santa Fe, Argentina<sup>2</sup>Estación Biológica Corrientes (CONICET), Corrientes, Argentina<sup>3</sup>Universidad Nacional de General Sarmiento, Buenos Aires, Argentina<sup>4</sup>Facultad de Humanidades y Ciencias, Universidad Nacional del Litoral, Santa Fe, Argentina

In this study, we examined the influence of demography and social context on mother-offspring conflict in wild black and gold howler monkeys (*Alouatta caraya*) inhabiting two nearby sites in northern Argentina, one comprising continuous forest and one fragmented forest. These sites differed in population density (3.25 vs. 1.04 individuals/ha), degree of home range overlap between neighboring groups (70 vs. 31%), and rate of intergroup encounters (2 vs. 0.02–1 encounters/day), though not in interbirth interval or rate of infant mortality. During a 27-month study (September 2008 through November 2010), we observed 37 mother-offspring dyads across the two sites. We found a very similar pattern of mother-offspring conflict in both populations; specifically, the sites did not differ in any of the variables used to characterize the mother-offspring relationship (the time spent in contact, the rate at which the mother makes and breaks contact, the rate at which the infant breaks contact, the rate of maternal rejection, and signs of infant distress) except one (the rate at which the infant makes contact). Although mother-offspring conflict is a dynamic process that varies over time, our results suggest that the different demographic and social contexts found at the two study sites did not have a marked effect on quantitative aspects of the mother-offspring relationship in these populations of black and gold howlers. Finally, this study suggests that the environmental variability (ecological, demographic, and social traits) leads to a set of strategies used both by infants and mothers with a main goal of conflict resolution, with mothers specifically aiming to cope with the tradeoff between current and future reproduction. *Am. J. Primatol.* 77:911–923, 2015. © 2015 Wiley Periodicals, Inc.

**Key words:** mother-infant relationship; parent-offspring conflict; demography; social interactions; *Alouatta caraya*

## INTRODUCTION

During development, primate infants gradually become independent from their mothers with regard to feeding and locomotion. During this transition, mothers and infants begins to exhibit behavioral conflicts, mainly over the amount of parental investment given during the period of dependence and over the timing of termination of the dependence period [Altmann, 1980; Clutton-Brock, 1991; Trivers, 1974]. Despite the importance of the parental investment period for understanding the evolution of primate life histories and social behavior, the complex and dynamic interactions between mothers and infants that characterize the mother-infant relationship remain poorly understood [Maestriperi, 2002; Smieth et al., 2008]. Quantitative studies of the intensity and duration of parent-offspring conflict have been made for several African and Asian primates [*Cercopithecus aethiops*: Hauser and Fairbanks, 1988; *Macaca* spp.: Hinde, 1977; Gomendio,

1991; Deviney et al., 2003; *Papio* spp.: DeVore, 1963; Altmann, 1980; Lycett et al., 1998; *Trachypithecus leucocephalus*: Zhao et al., 2008; *Nycticebus coucang*: Ehrlich and MacBride, 1989; *Lemur catta*: Gould, 1990; *Pan troglodytes*: Horvat and Kraemer,

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1982; *Pongo pygmaeus*: Horr, 1977]. However, there have been very few such studies of parent-offspring conflict in Neotropical primates [but see *Callithrix jacchus*: Ingram, 1977; Locke-Haydon and Chalmers, 1983; *Alouatta caraya*: Pavé et al., 2010]. Overall, studies suggest that the most important variables to measure for describing the intensity of parent-offspring conflict are the rate of maternal rejection of infants, behavioral signs of infant distress, the amount of time mothers and offspring spend in contact, and the rate at which mothers and their offspring initiate and break contact [Gomendio, 1991; Hauser and Fairbanks, 1988; Horvat and Kraemer, 1982; Locke-Haydon and Chalmers, 1983; Schino et al., 2001]. It is considered, for example, that the conflict is intense when mothers increase the frequency of rejection in response to the infant attempts at suckling, resulting in an increased frequency of infant distress.

Some studies have shown that ecological and life-history traits, such as food availability and the length of the interbirth interval, affect the intensity and duration of parent-offspring conflict, but such studies are limited and focused on cercopithecines [Hauser and Fairbanks, 1988; Hill et al., 2000; Lee, 1987; Lycett et al., 1998]. For example, Hauser and Fairbanks [1988] studied mother-infant relationship in wild *Cercopithecus aethiops* inhabiting two environments—a dry woodland and a swamp—that varied in food availability. The swamp had consistent availability of high-quality food throughout the year (characterized by a high availability of a particular *Acacia* sp. whose resources comprised 50% of the diet), while the woodland was the less favorable environment because it was dominated by another *Acacia* sp. whose resources are poorer in quality. The study found that females ( $n = 14$ ) living in the swamp exhibited shorter interbirth intervals (1 vs. 2 yr) and higher conflict levels with their offspring (higher rates of maternal rejection and attempts to make contact by infants) in comparison to females ( $n = 10$ ) from the woodland.

Other factors that may influence the conflict between mothers and offspring over the extent and timing of parental investment includes the age of the mother, the mother's resumption of sexual activity, and the conception and birth of new siblings [Deviney et al., 2003; DeVore, 1963; Gomendio, 1991; Horr, 1977; Jay, 1963; Lee, 1987; Nash, 1978; Pavé et al., 2010; Schino et al., 2001; Trivers, 1974]. For example, in captive *Macaca mulatta*, infant distress (measured by frequency of screams and tantrums) studied in 12 mother-infant dyads increased about 50% when mothers returned to sexual activity [Gomendio, 1991]. Similarly, in a preliminary study of mother-offspring conflict in wild *Alouatta caraya*, 100% of suckling attempts ( $n = 3$  infants) were rejected by mothers after the birth of new siblings [see Pavé et al., 2010 for details]. However, we lack strong empirical

data to explore how other social traits, such as the social interactions between neighboring groups and the demographic traits of primate populations affect the intensity of parent-offspring conflict [Maestripieri, 2002]. For example, captive *Macaca mulatta* mothers ( $n = 28$ ) differed in the rate at which they rejected (1 rejection/hr vs. 1.5 rejection/hr) and restrained their offspring (4.5 restraining/hr vs. 1.2 restraining/hr) according to level of kidnapping and harassment they experienced, both of which are associated with the local population density of the groups (0.5 individuals/m<sup>2</sup> vs. 0.06 individuals/m<sup>2</sup>) [Maestripieri, 2001]. In groups with higher density, mothers restrained their infants more frequently (i.e. attempted to prevent infants from breaking contact) and less frequently rejected their infants than in groups with lower density. Maestripieri [2001] argued that in the higher density groups, the increased maternal restraining behavior may reduce the kidnapping and harassment attempts of infants by other group members [Maestripieri, 2001]. Although the above study is a good approximation to assess how demographic and social conditions affect mother-offspring relationship, the results may be highly influenced by captivity.

In this study, we present data on mother-infant relationships in two wild populations of black and gold howler monkeys (*Alouatta caraya*) living at this taxon's southernmost geographic distribution in forests of northern Argentina. These howler populations are excellent subjects for this study because they live in forests that vary in certain ecological, demographic, and social dimensions (Table I). Our goals are to examine the influence of population density, degree of home range overlap, and rate of intergroup encounters on the expression of parent-offspring conflict in black and gold howler monkeys and to provide new data on the expression of mother-offspring conflict in primates living in wild environments.

Data were collected over a 27-month period in a continuous flooded forest on an island of the Parana River and in a nearby fragmented semi-deciduous forest on the mainland. Previous studies have provided evidence of mother-offspring conflict at both study sites [Pavé et al., 2010; Raguét-Schofield and Pavé, 2015]. For example, a preliminary study on 2 infants (between 0 and 11 months) and 3 juveniles (between 12 and 29 months) from the island showed that all immature individuals received maternal rejection of suckling and transport and that the presence of newborns affected negatively the mother-infant relationship [Pavé et al., 2010]. Similarly, on the mainland we found that mothers likewise rejected the attempts during suckling and transport of 18 infants studied across the 12 months of the infancy [Raguét-Schofield and Pavé, 2015]. Previous studies have also shown that food availability varies between the sites (Table I);

TABLE I. Ecological, Demographical, and Social Situations of the Study Sites

|  | Isla Brasilera<br>(Flooded forest)                     | San Cayetano<br>(Mainland forest)                                | Source     |
|--|--|--|------------|
| Habitat  | Continuous forest                                      | Fragmented forest  | 1–4        |
| Vegetation<br>(Richness and diversity of plants) | 53 spp.; H' index, range = 1–2.5                       | 61 spp.; H' index, range = 1–13                                  | 1–8        |
| Predation  | None   | Low level (3)  | 3–5, 12    |
| Food availability<br>(monthly average)           | High and constant<br>throughout the year (59%)         | Low throughout the<br>year and seasonal<br>(fall in winter) (9%) | 2–3, 6     |
| Social structure of groups<br>(average)          | Mainly multi-male multi-female (65%)                   | Mainly uni-male multi-female (72%)                               | 1–5        |
| Overlapping of home range<br>(average)           | 70%  | 31%  | 3, 6, 9    |
| Rate of intergroup encounter<br>(average)        | 2 encounters/day                                       | 0.02–1 encounters/day  | 3, 9       |
| Population density<br>(average)                  | 3.25 individuals/ha                                    | 1.04 individuals/ha  | 2, 4       |
| Group size (average)                             | 9.7 individuals  | 6.8 individuals  | 2, 4       |
| Home range size<br>(average)                     | 4.6 ha   | 7 ha   | 3, 6, 9–10 |
| Births   | Throughout the year, with or<br>without peak in winter | Seasonal, peaks in<br>autumn-winter                              | 2, 5–7     |
| Interbirth interval                              | 14.07 ± 1.9 mo   | 15 ± 3.6 mo  | 1, 5–6     |
| Infant mortality<br>(average)                    | 38%  | 35%  | 1, 5       |
| Infanticide<br>(average)                         | 18.6%  | 25%  | 5, 11      |

References: 1: Rumiz, (1990); 2: Kowalewski and Zunino, (2004); 3: Kowalewski, (2007); 4: Zunino et al., (2007); 5: Pavé et al., (2012); 6: Pavé, (2013); 7: Zunino, (1996); 8: Fernández, (2014); 9: Raño, (2010); 10: Zunino, (1989); 11: Zunino et al., (1986); 12: Kowalewski personal observation.

food is more seasonal in the fragmented forest. Although food availability was reported to be an important factor influencing the length of the interbirth interval (IBI) in some primate species [Hauser and Fairbanks, 1988; Hill et al., 2000; Lee, 1987; Lycett et al., 1988] in our study sites females do not differ in the length of the IBI and infant mortality is similar (Table I). We assumed, therefore, that differences in food availability would not directly influence the behavioral patterns of the howler groups at either sites because neither site experiences dramatic reductions in food availability, and howler monkeys are capable of balancing nutrient intake over periods of days, weeks, or months by principally consuming a single food type [Fernández, 2014; Garber et al., 2015]. Both adult males and females with or without dependent infants participate in intergroup encounters [Kowalewski, 2007; Kowalewski and Garber, 2015]. The main differences between the sites is that in the continuous forest there is higher number of multi-male multi-female groups and higher degree of home ranges overlap compared with the fragmented forest in the mainland where there is higher prevalence of uni-male multi-female groups and these groups share less of 50% of their home ranges (Table I).

Based on our preliminary data and data from literature [Kowalewski and Zunino, 2004; Kowalewski and Garber, 2010; Maestriperi, 2001, 2002; Pavé et al., 2010, 2012; Raguet-Schofield and Pavé, 2015], we test a series of predictions with respect to the effect of population density, home range overlap between neighboring groups, and rate of intergroup encounters relative to the intensity of parent-offspring conflict. If the higher population density, more highly overlapping home ranges, and higher rate of intergroup encounters in the continuous forest encourages mothers to take a more active role in group social interactions (and therefore be less willing to invest time on their offspring compared with the mothers of the fragmented forest), then we expect that mothers of the continuous forest will invest less time in contact with their offspring, initiate contact less frequently, break contact more frequently, and have higher rejection rates to their infants, compared with mothers living in the fragmented forest. Moreover, we predict that the higher population density and differing social situation in the continuous forest encourages infants to follow their mothers and attempt to remain with them for a significantly longer time period. We therefore expect that infants living in the continuous forest will try to initiate contact with their mothers

more frequently, break contact less frequently, and spend longer time of distress than infants in the fragmented forest.

## METHODS

### Study Site

We studied groups in two populations of *Alouatta caraya* in northern Argentina: 5 groups on Isla Brasilera, Chaco Province (27°18'S, 58°38'W) and 6 groups at a mainland site located in San Cayetano, Corrientes Province (27°30'S, 58°41'W). The sites are 27 km from each other and they do not vary substantively in temperature, precipitation, or photoperiod [Rumiz, 1990]. The climate at both sites is subtropical with a mean annual temperature of 21.6°C and a mean annual rainfall of 1,200 mm (Servicio Meteorológico Nacional de Argentina). Isla Brasilera has an area of 292 ha and is located near the confluence of the Paraná and Paraguay Rivers. The area experiences at least one flooding event annually that varies in intensity and duration, lasting from a few days to several months [Neiff et al., 1985]. At this site, howlers live in a continuous forest. The principal known causes of infant deaths are floods that affect the production of mature leaves and attacks by adult males during male replacements [Pavé et al., 2012]. At San Cayetano, howlers live in a fragmented and semi-deciduous forest. The main known cause of infant mortality at San Cayetano is attack by adult males during male replacements [Pavé, 2013; Rumiz, 1990]. Table I shows the main traits of both study sites.

### Focal Subjects

We studied the behavior of 37 mother-infant dyads. At Isla Brasilera, 16 dyads from 5 groups with a mean home range of  $4.08 \pm 1.01$  ha were included. All the study groups overlapped their home range (range = 50–80%) with at least 2 or 3 neighboring groups. The 21 dyads of San Cayetano belonged to 6 groups with a mean home range of  $7.26 \pm 4.09$  ha, and the groups overlapped their home range with 1 to 3 neighboring groups (range = 0–75%), except one group that exclusively used 2 fragments of forest. Groups at Isla Brasilera were 60% multimale–multifemale (with 2–3 adult males and 3 adult females) and 40% unimale–multifemale (with 1 adult male and 2–3 adult females); at San Cayetano, 16.7% of the groups were multimale–multifemale (with 2 adult males and 4 adult females) and 83.3% unimale–multifemale (with 1 adult male and 2–3 adult females). At both sites, all mothers were multiparous, identified by signs of previous nursing, i.e. elongated nipples. In all study groups there was some type of allomaternal care, i.e. transport, care/comfort, allosuckling, and allogrooming [see Pavé, 2013]. Following Rumiz [1990] we defined the infant period from birth to 1 yr of age. Infants were

studied beginning during the month of birth ( $n = 11$  infants from San Cayetano and 4 infants from Isla Brasilera) or in months after birth ( $n = 10$  infants from San Cayetano beginning between months 1 and 6, and 12 infants from Isla Brasilera beginning between months 1 and 8). In all the cases, the infants were studied up to one year of life or until their disappearance, death, or physical injury. We studied 10 female infants and 11 male infants at San Cayetano and 4 female infants, 10 male infants, and 2 infants of unknown sex (studied during their two first months of life) at Isla Brasilera. We identified individual howlers by age, sex, and natural and/or artificial markings (color anklets and ear tags). We assigned age categories following Rumiz [1990] based on genital development, estimated body size, and coloration.

### Behavioral Data

We simultaneously used focal and instantaneous point sampling techniques [Altmann, 1974; Table II]. Focal data were collected on a monthly basis, assigning an observation day per dyad per month of life of the infants, from sunrise to dusk (from 6:20 to 19:30 hr in summer and 7:30 to 18:30 hr in winter). Point samples were taken every 5 min during the focal sampling. We assigned 1 day of observation per dyad mainly by logistic issues, such as the daily search of the study groups; however, we took the caution of following the monkeys in similar days with respect to the weather in each season. We collected a total of 2,297 hr of focal observations (1,586 hr for San Cayetano and 711 hr for Isla Brasilera), i.e. approximately  $10 \pm 1.5$  hr of observation per infant per month of life. Additionally, we obtained 27,588 instantaneous point samples (19,081 points for San Cayetano and 8,507 for Isla Brasilera), or approximately 100 points per infant per month of life. Behavioral categories used to characterize the mother-infant relationship and to quantify the degree of mother-infant conflict (Table II) were taken from previous studies [Gomendio, 1991; Hauser and Fairbanks, 1988; Horvat and Kraemer, 1982; Locke-Haydon and Chalmers, 1983; Pavé et al., 2010; Schino et al., 2001]. Make and break contact were analyzed between mo 2 and 11 of infancy because during the two first months of life (mo 0 and 1) infants spend nearly all of their time in contact with their mothers. We calculated the relative frequency of maternal rejection between mo 1 and 11 of infancy using only suckling attempts because these were more conspicuous than solicitations for care/comfort and transport.

### Data Analyses

Each infant was represented by a different number of hours of focal observation and instantaneous point sampling because the time of observation

TABLE II. Behavioral Categories Used to Estimate Mother-Infant Conflict and Methods of Recording

| Behavior                                 | Description  | Recording methods |
|--|--|-------------------|
| Time in contact                          | When the infant is in any type of contact with its mother (i.e. ventral, dorsal, or lateral contact) or when the infant is on a branch but still in physical contact with its mother   | Point samples     |
| Mother make contact (MMC)                | When the mother initiates physical contact with the infant   | Focal samples     |
| Mother break contact (MBC)               | When the mother terminates physical contact with the infant  | Focal samples     |
| Infant make contact (IMC)                | When the infant initiates physical contact with the mother   | Focal samples     |
| Infant break contact (IBC)               | When the infant terminates physical contact with the mother  | Focal samples     |
| Absolute frequency of maternal rejection | All the instances in which mothers rejects their offspring (i.e. in context of suckling, care/comfort, and transport) and when mothers finishes a bout of suckling or transport  | Focal samples     |
| Relative frequency of maternal rejection | This variable reflects the proportion of suckling attempts that mothers rejects and was obtained by dividing the frequency of maternal rejections by the frequency of total suckling attempts  | Focal samples     |
| Suckling attempt (SA)                    | When the infant touches or bit its mother's body in the area near of the nipple; whimpers and tries to gain access to the nipple; or moves its mouth toward the nipple. During a rejection event of suckling, mothers prevents the infants from making contact or gaining access to the nipple, or they pushes the infant away | Focal samples     |
| Infant distress                          | When the infant gives loud vocalizations and/or jerking, screaming, and/or biting the mother in response to mother rejection or by absence of response from the mother.  | Focal samples     |

differed between the seasons (11 hr in spring, 12 hr in summer, 11 hr in autumn, and 10 hr in winter) and sometimes infants were lost during the observations. For these reasons, the frequency of make and break contact by mothers and infants, the frequency of suckling attempts, the frequency of maternal rejection, and the time spent in distress obtained per infant per age were divided by the total time of activity obtained per infant per age (corresponding to one full day per month of life equivalent to 10–12 hr, depending on each season). The same adjustment was made for the time in contact obtained from the point samples.

For comparisons within each study site (between the ages of the infant period) and between the study sites with respect to the variables used to quantify parent-offspring conflict, we used a generalized linear mixed model (GLMM) [Zuur et al., 2009]. This analysis controls for repeated measures on the same infant studied at different ages and incorporates both fixed and random effects. In the models, the response variables were the proportions of time spent in contact, time spent in infant distress, frequency of rejection, and frequency of make and break contact by mothers and infants. In the models within each study site, the predictor variable (fixed

factor) was only the age of the infants. In the models comparing the two study sites, the predictor variables were the ages of the infants and the study sites. In both kinds of models, the random factors were the identity of the infants (16 infants at Isla Brasilera and 21 infants at San Cayetano) nested within the groups to which the infants belonged. We considered  $P \leq 0.05$  as the criterion for significance for all statistical tests. We performed the statistical analyses with InfoStat 2013 [Di Rienzo et al., 2013] and R version 3.0.3 (R Development Core Team 2013) with the MASS package. This research complied with the current laws and regulations of Argentina and was conducted with permission from the National Resources Board, Fauna and Flora Department, Corrientes Province, Argentina. This research also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Primates.

## RESULTS

### Time in Contact

During the month of birth (mo 0) infants were in contact with their mothers  $99.6 \pm 1\%$  ( $n = 11$ ) of the time at San Cayetano and  $99.4 \pm 1.1\%$  ( $n = 4$ ) at Isla

Brasileira (Fig. 1). When infants were not in contact with their mothers during mo 0, they were less than 1 m from them and engaging in either exploration or in contact with other group member. By mo 1, the time in contact began to decrease gradually and by mo 11, infants spent only  $16.8 \pm 17.5\%$  in contact with their mothers at San Cayetano (range = 0–55.6%,  $n = 15$ ) and  $24.7 \pm 19.2\%$  at Isla Brasileira (range = 14.3–62.9%,  $n = 5$ ). The interaction between site and age did not affect this variable of mother-infant proximity; nor did we find differences between the study sites as we had predicted (Table III). However, the time in contact decreased significantly with the infant age (Table III). The model for each study site with only the age as fixed factor showed that the age of the infants significantly influenced the time in contact at San Cayetano (GLMM:  $t = -13.038$ ,  $P = <0.001$ ,  $n = 154$ ) and at Isla Brasileira (GLMM:  $t = -7.943$ ,  $P = <0.001$ ,  $n = 70$ ). Therefore, at both study sites we found a similar pattern in the monthly variation of the time in contact between mothers and offspring.

### Make and Break Contact by Mothers

At both study sites, mothers broke contact more than they made contact with their infants during the infant period, with the exception of mo 2 (Fig. 2a and 2c). In mo 2, we found that the frequency of MMC and MBC was the same. These contacts mainly included mothers retrieving their offspring back from other group members, when infants were left behind during group displacements, and/or when infants moved away to explore the environment. The rate of MBC increased from mo 3 with peaks in mo 7 at San

Cayetano ( $2 \pm 1.6$  contacts/day) and mo 5 at Isla Brasileira ( $3.4 \pm 0.7$  contacts/day), after which MBC gradually decreased because infants naturally made less contact with their mothers. The interaction between site and age did not affect MMC (Table III). Although we did not find differences between the study sites in MMC (Table III), the frequency of MMC depended significantly on infant age (Table III), and infant age significantly affected this variable at both study sites (GLMM for San Cayetano:  $t = -2.722$ ,  $P = 0.007$ ,  $n = 134$ ; GLMM for Isla Brasileira:  $t = -3.315$ ,  $P = 0.002$ ,  $n = 60$ ). With respect to MBC, the model with the interaction between site and age affected this variable (Table III). MBC also differed significantly between the ages of the infant period but not between the sites (Table III). The age of the infants affected this variable only at Isla Brasileira (GLMM:  $t = 3.239$ ,  $P = 0.002$ ,  $n = 60$ ).

### Make and Break Contact by Infants

At both study sites, infants made contact with their mothers more frequently than they broke contact between mo 3 and 11 (Fig. 2b and 2d). However, in mo 2 infants broke more contact than they made. This difference was mainly because at this age infants began to move away small distances (<1 m) from their mothers to explore the environment. Also, at both study sites, the frequency of IMC and IBC gradually decreased after mo 5, although for the two variables the difference between ages was more marked at San Cayetano when compared with Isla Brasileira. The peaks of IMC in mo 7 at San Cayetano and in mo 5 at Isla Brasileira coincided with

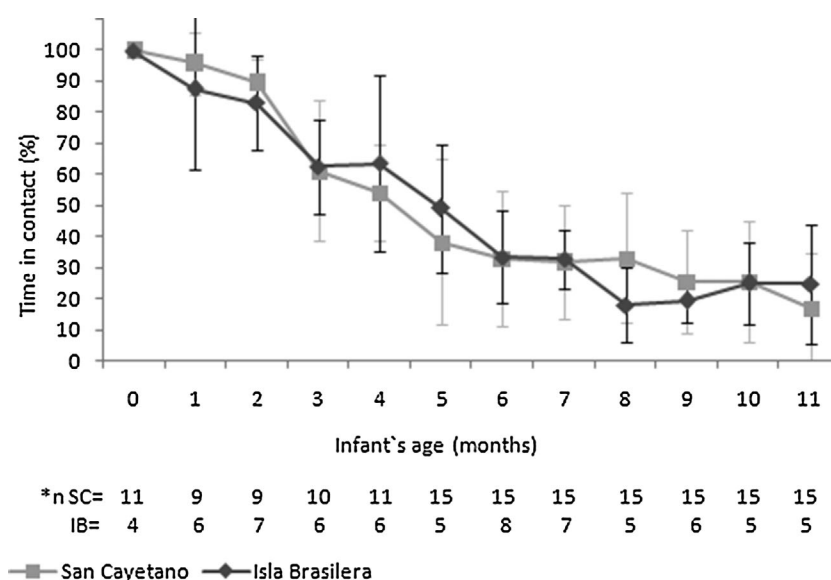


Fig. 1. Mean proportion per day of observation of time in contact (in %) between infants and their mothers during the infant period by study site. The points represent the mean values ( $\pm$  SD) of all infants present by age. \* $n$  = number of infants contributing to each age of the infant period to both study sites.

**TABLE III. Results from the Glmm for the Effect of Age in Months of the Infants and the Study Sites (Fixed Factors) on Time in Contact, Maternal Rejection, Infant Distress, and Make and Break Contact by Mothers and Infants. The Identity of the Infants and the Groups to Which They Belonged Were Incorporated as Random Factors**

|                                     | $\beta \pm \text{S.E}$ | DF  | t       | p        |
|-------------------------------------|------------------------|-----|---------|----------|
| Time in contact                     |                        |     |         |          |
| Intercept                           | 1.8484 ± 0.3263        | 185 | 5.664   | <0.0001* |
| Site                                | 0.1908 ± 0.4073        | 9   | 0.468   | 0.6506   |
| Age                                 | -0.3489 ± 0.0480       | 185 | -7.267  | <0.0001* |
| Site* age                           | -0.0173 ± 0.0557       | 185 | -0.311  | 0.7559   |
| Variance of random factors = 0.4473 |                        |     |         |          |
| Mother makes contact                |                        |     |         |          |
| Intercept                           | -9.3267 ± 0.3605       | 162 | -25.874 | <0.0001* |
| Site                                | -0.6092 ± 0.4635       | 9   | -1.314  | 0.2212   |
| Age                                 | -0.1739 ± 0.0567       | 162 | -3.068  | 0.0025*  |
| Site* age                           | 0.0629 ± 0.0682        | 162 | 0.923   | 0.3576   |
| Variance of random factors = 0.5169 |                        |     |         |          |
| Mother breaks contact               |                        |     |         |          |
| Intercept                           | -8.4256 ± 0.3109       | 162 | -27.099 | <0.0001* |
| Site                                | 0.3316 ± 0.3986        | 9   | 0.832   | 0.4270   |
| Age                                 | 0.1118 ± 0.0362        | 162 | 3.088   | 0.0024*  |
| Site* Age                           | -0.1169 ± 0.0434       | 162 | -2.696  | 0.0078*  |
| Variance of random factors = 0.2558 |                        |     |         |          |
| Infant makes contact                |                        |     |         |          |
| Intercept                           | -6.9323 ± 0.1945       | 162 | -35.644 | <0.0001* |
| Site                                | 0.6070 ± 0.2417        | 9   | 2.5118  | 0.0332*  |
| Age                                 | -0.0350 ± 0.0264       | 162 | -1.3288 | 0.1858   |
| Site* age                           | -0.1197 ± 0.0312       | 162 | -3.8385 | 0.0002*  |
| Variance of random factors = 0.2116 |                        |     |         |          |
| Infant breaks contact               |                        |     |         |          |
| Intercept                           | -6.6129 ± 0.2299       | 162 | -28.753 | <0.0001* |
| Site                                | 0.4311 ± 0.2741        | 9   | 1.573   | 0.1503   |
| Age                                 | -0.2581 ± 0.0404       | 162 | -6.383  | <0.0001* |
| Site* age                           | -0.0235 ± 0.0461       | 162 | -0.511  | 0.6104   |
| Variance of random factors = 0.3132 |                        |     |         |          |
| Maternal rejection                  |                        |     |         |          |
| Intercept                           | -2.9532 ± 0.3036       | 185 | -9.728  | <0.0001* |
| Site                                | 0.3637 ± 0.3668        | 9   | 0.991   | 0.3473   |
| Age                                 | 0.0926 ± 0.0430        | 185 | 2.153   | 0.0325*  |
| Site* age                           | -0.082 ± 0.0514        | 185 | -1.596  | 0.1120   |
| Variance of random factors = 0.2369 |                        |     |         |          |
| Infant distress                     |                        |     |         |          |
| Intercept                           | -4.4917 ± 0.3708       | 185 | -1.211  | <0.0001* |
| Site                                | -0.3132 ± 0.5074       | 9   | -0.617  | 0.5523   |
| Age                                 | 0.1084 ± 0.0456        | 185 | 2.376   | 0.0185*  |
| Site* age                           | -0.1576 ± 0.0610       | 185 | -2.582  | 0.0106*  |
| Variance of random factors = 0.5343 |                        |     |         |          |

\*Indicate statistically significant effect of a factor and/or interaction of factors in the model.

peaks in MBC during these months (Fig. 2). Thus, these results suggest that infants at both study sites were responsible for making contact with their mothers more often than they broke it. For IMC, the interaction between age and site was significant and there were significant differences between the sites, but not among the ages of the infants (Table III). It is important to note that in the model for each study site, IMC depended significantly on infant age only at San Cayetano (GLMM:  $t = -8.969$ ,  $P < 0.001$ ,  $n = 134$ ) while at Isla Brasilera, age did not significantly influence the frequency of IMC. These

results suggest that infants from the two study sites varied in their tendency to make contact with their mothers. With respect to IBC, the interaction between study site and age did not affect this variable and also this variable was independent from the study sites (Table III). However, IBC depended of the age of the infants (Table III). In the model for each study site, IBC differed significantly across ages at both study sites (GLMM for San Cayetano:  $t = -12.677$ ,  $P < 0.001$ ,  $n = 134$ ; GLMM for Isla Brasilera:  $t = -6.052$ ,  $P < 0.001$ ,  $n = 60$ ). These results suggest that at both study sites, infants broke

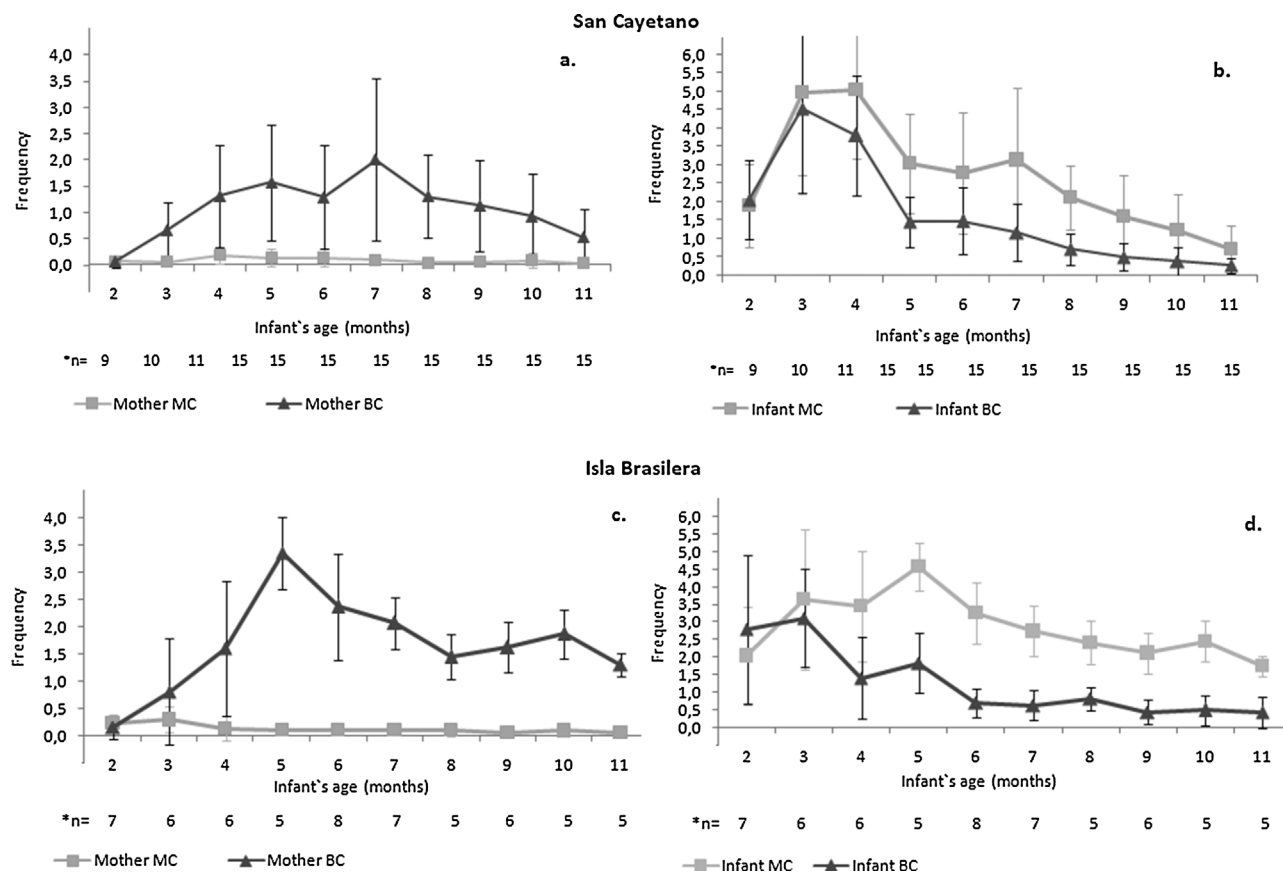


Fig. 2. Mean frequency per day of observation of mothers make and break contact with their infants (a and c) and infants make and break contact with their mothers (b and d) during the infant period by study site. The points represent the mean values ( $\pm$  SD) of all infants present by age. \*n = number of infants contributing to each age of the infant period to both study sites.

more contact with their mothers during the first months of life (in which they spend much of their time in exploration), and from mo 5, infants broke contact less with their mothers as they become more independent.

### Maternal Rejection

Maternal rejection of suckling, transport, and care/comfort occurred throughout the infant period at both study sites. At San Cayetano, maternal rejection occurred between the month of birth until mo 11 and at Isla Brasilera, between mo 1 and 11 (Fig. 3). At both sites, higher frequencies of maternal rejection occurred between mo 3 and 7, although there was considerable variation among individuals during this period (Fig. 3). At San Cayetano, higher values occurred in mo 4 and 7 ( $14.5 \pm 10.3\%$  and  $14 \pm 10.6\%$  respectively) and at Isla Brasilera there was a peak in mo 5 ( $17.2 \pm 6.9\%$ ). Considering the results of maternal rejection and the contribution of mothers and infants to make and break contact (Fig. 3 and 4), a similar pattern arises at both study sites. At San Cayetano, the increase of IMC between

mo 3 and 7, compared with the rest of the ages, coincided with a gradual increase of maternal rejection and MBC. Similarly at Isla Brasilera, the peak of IMC coincided with peaks of maternal rejection and MBC in mo 5. In other words, during periods of high interaction between mothers and infants, many infant attempts to elicit maternal care (i.e. suckling, transport, and care/comfort) resulted in maternal rejection.

We show the suckling attempts accepted and rejected by mothers at both study sites in Figure 4. At San Cayetano, infant suckling attempts gradually increased until mo 7 and then began to decrease until the end of the infant period. Mothers accepted most suckling attempts until mo 6; afterwards, the primary maternal response was rejection. This pattern became even more evident during mo 11, when 84.5% of attempts were rejected. At Isla Brasilera, suckling attempts fluctuated throughout the infant period. Results indicate that months with the highest number of suckling attempts (mo 3, 6, 7, 9, and 10) coincided with the highest instances of maternal rejection. At this study site, the highest number of suckling attempts occurred in mo 9



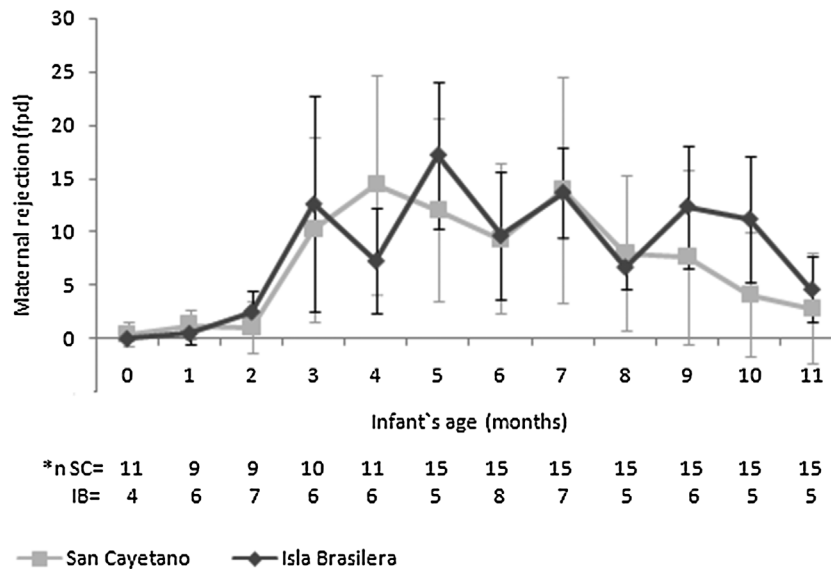


Fig. 3. Mean frequency per day of observation (fpd) of maternal rejection during the infant period by study site. The points represent the mean values ( $\pm$ SD) of all infants present by age. \*n = number of infants contributing to each age of the infant period to both study sites.

( $10.3 \pm 5.3$  SA; range = 1–17;  $n = 6$  infants) and mo 10 ( $8.6 \pm 2.9$  SA; range = 1–17;  $n = 5$  infants). Possibly because mothers did not have new infants when their current infants were near the end of the infant period, they allowed to the current infants to suckle. Maternal rejection was not affected by the interaction of age and site, nor did we find differences between study sites as predicted (Table III). However, the frequency of maternal rejection depended significantly on the infant age (Table III), though infant age significantly affected the frequency of maternal rejection only at Isla Brasilera (GLMM:  $t = 2.704$ ,  $P = 0.009$ ,  $n = 70$ ).

### Infant Distress

At both study sites, infant distress was evident during all months of the infant period, but the levels of distress peaked between mo 3 and 8 (Fig. 5). At San Cayetano, the highest values were recorded during mo 5 and 8 and at Isla Brasilera, between mo 4 and 7. Differences between the ages were more marked at Isla Brasilera than at San Cayetano. In fact, the analysis of GLMM indicated that age affected infant distress only at Isla Brasilera (GLMM:  $t = 2.229$ ,  $P = 0.03$ ,  $n = 70$ ). Many instances of infant distress were not a response to maternal rejection (Fig. 3); rather, increased levels of infant distress occurred during group displacements in the context of intergroup encounters or when mothers moved away during a feeding bout and the infants had to move independently to follow them instead of being carried. The analysis of infant distress using GLMM indicated that the interaction between site and age affected this variable (Table III) and there

were significant differences across ages of the infant period (Table III), however infant distress was independent of the study sites (Table III).

### DISCUSSION

Based on previous studies, we predicted that differences in population density, degree of home range overlap, and rate of intergroup encounters between our two study sites would result in differences in the intensity of parent-offspring conflict (measured by time in contact, MMC, MBC, IMC, IBC, maternal rejection, and infant distress). In contrast to our predictions, we found that only one of our measures of mother-infant conflict, IMC, differed between the sites. We did not find significant differences in time in contact, MMC, MBC, IBC, maternal rejection, or infant distress (Table III). This lack of difference in the intensity of the mother-offspring conflict could be a consequence of the lack of differences of IBI between the study sites (Table I), because several studies in cercopithecines have shown that the length of IBI could affect the time of maternal investment, i.e. when the IBI is shorter, the maternal investment in the current offspring is low and in consequences the conflict between the dyad is high [Gomendio 1991; Hauser and Fairbanks, 1988; Hill et al., 2000; Lee, 1987; Lycett et al., 1988].

It is important to note that time in contact of the mother-infant dyad at both study sites followed the same pattern reported in a wide range of non-human primates: as the age of the infant increases, the time in contact with the mother decreases [e.g. *Alouatta palliata*: Clarke, 1990; *Brachyteles arachnoides*: Odalia-Rmoli and Otta, 1997; *Cercopithecus aethiops*:

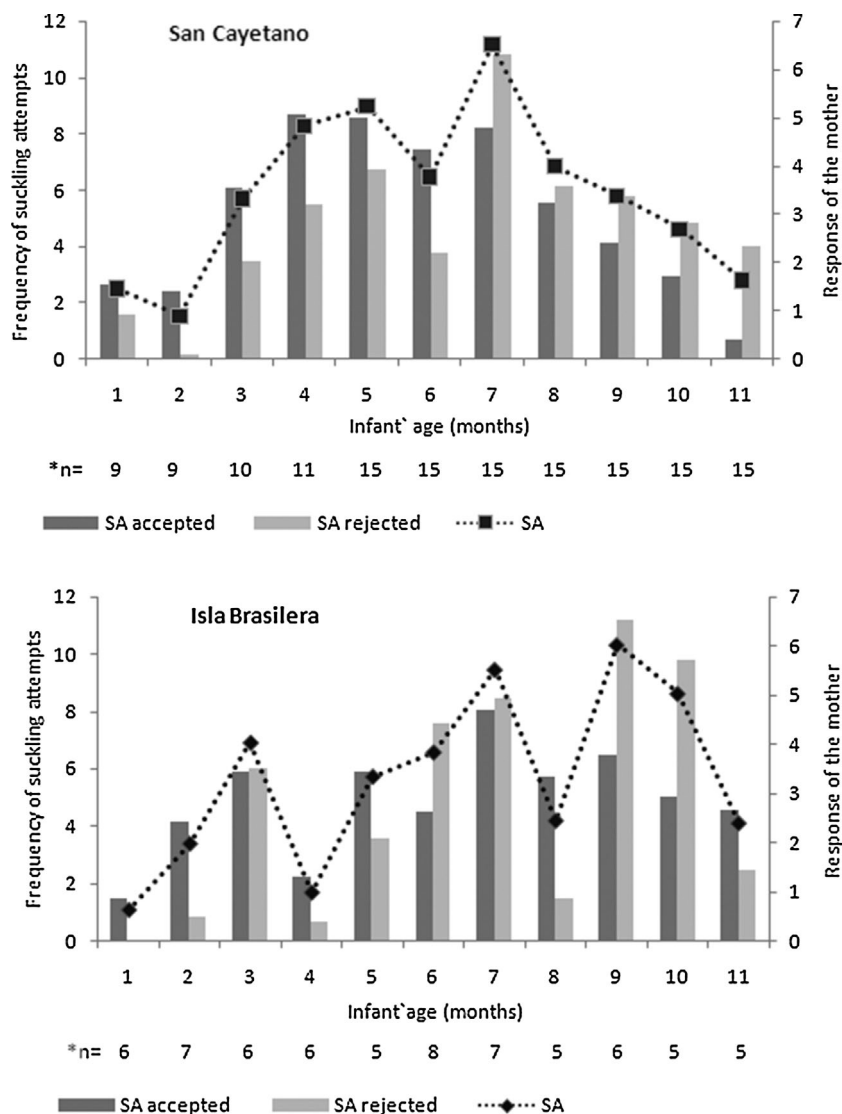


Fig. 4. Mean frequency of suckling attempts (SA) per day of observation by infants and the mean response of the mothers (SA accepted or SA rejected) during the infant period by study site. The points and the length of the bars represent the mean values of all infants present by age. \*n = number of infants contributing to each age of the infant period to both study sites.

Hauser and Fairbanks, 1988; *Papio cynocephalus*: Altmann, 1980; *Macaca mulatta*: Johnson, 1986; *Rhinopithecus bieti*: Li et al., 2013; *Trachypithecus leucocephalus*: Zhao et al., 2008; *Lemur catta*: Gould, 1990; *Eulemur flavifrons*: Volampeno et al., 2011; *Gorilla gorilla gorilla*: Nowell and Fletcher, 2007]. In both of our study sites, infants initiated contact more frequently than they broke it throughout the infant period, except for mo 2 when infants moved small distances from their mothers mainly to explore the environment. Similar results have been reported in other primates [*Alouatta palliata*: Clarke, 1990; *Cercopithecus aethiops*: Hauser and Fairbanks, 1988; *Cercopithecus mitis*: Forster and Cords, 2003; *Papio cynocephalus*: Altmann, 1980]. These results suggest that infants are primarily responsible for promoting the contact with their mothers.

Mothers broke contact more frequently than they made contact with their offspring and rejected infants throughout the entire infant period. The same pattern has been found in other non-human primates [*Alouatta palliata*: Clarke, 1990; *Cercopithecus aethiops*: Hauser and Fairbanks, 1988; *Papio cynocephalus*: Altmann, 1980; *Rhinopithecus bieti*: Li et al., 2013; *Trachypithecus leucocephalus*: Zhao et al., 2008], suggesting that these maternal behaviors serve to promote infant independence. At both study sites, maternal rejection, including rejection of suckling attempts, was higher between mo 3 and 7. Only at Isla Brasilera did we find that maternal rejection depended on infant age. These results suggest that although maternal rejection persisted until mo 11, the higher frequency of MBC and increasing of rejection between mo 3 and 7 are

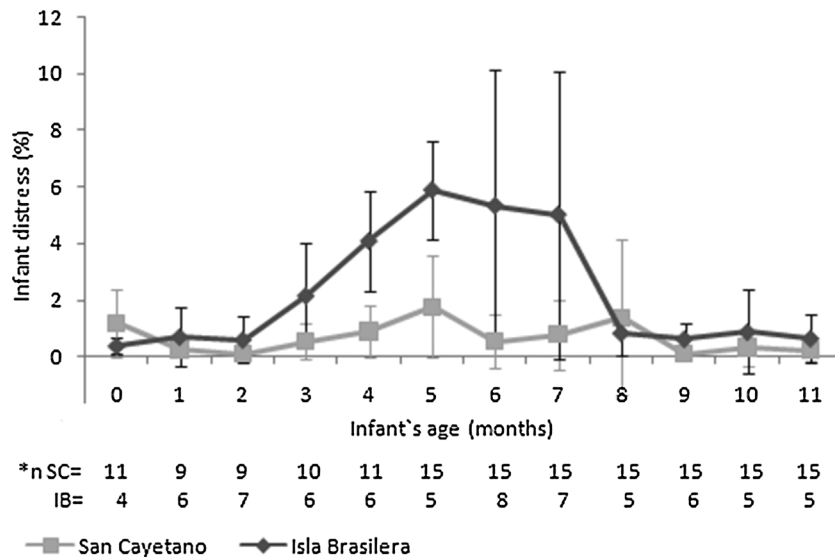


Fig. 5. Mean proportion per day of observation of infant distress by infant's age and study site (in %). The points represent the mean values ( $\pm$  SD) of all infants present by age. \*n = number of infants contributing to each age of the infant period to both study sites.

possibly a strategy to promote infant independence rather than to terminate maternal investment. This pattern has also been observed in other primate species [*Cercopithecus mitis*: Forster and Cords, 2003; *Papio cynocephalus*: Altmann, 1980; *Trachypithecus leucocephalus*: Zhao et al., 2008] and is consistent with parent-offspring theory [Trivers, 1974], which predicts that infants demand longer duration of parental care during the period of dependence and a longer period of parental care ending dependency. Infants expressed distress throughout the infant period; however distress was not always associated with maternal rejection. For example, infant distress at Isla Brasilera increased between mo 4 and 7 but maternal rejection was higher in mo 5 and 7 and lower in mo 4 and 6. Conversely, we recorded low values of infant distress in mo 9 and 10, but high values of maternal rejection during these months (Fig. 3 and 5). A similar pattern occurred at San Cayetano. Also at Isla Brasilera, the time invested in infant distress varied significantly with the infant age. Compared with San Cayetano, infant distress at Isla Brasilera was higher between mo 3 and 7 but there were no differences between the sites during the entire infant period. The distress call at Isla Brasilera generally occurred when infants had to move independently to follow their mothers. This behavior was also observed in infants of *A. palliata* of 6 mo in Panama ( $n = 26$  infants) at the beginning of group displacements when infants were left behind by their mothers [Baldwin and Baldwin, 1973]. We recorded lower values of infant distress at both study sites from mo 8, possibly because infants began to interact more with other group members at this point and had less difficulty following group displacements on their own.

Our results, however, showed differences in the frequency of IMC between the sites. At Isla Brasilera, this variable remained relatively constant throughout the infant period, suggesting that these infants were more highly motivated than infants at San Cayetano to stay in contact with their mothers from birth to the last month of infancy. This difference may be related to demographic and social traits of Isla Brasilera compared with San Cayetano, including higher population density of howlers, greater overlap in home ranges between neighboring groups, and higher rate of intergroup encounters (Table I). This combination of factors results in infants being left behind during group displacements, where they are exposed to other groups or solitary individuals, increasing the chances of agonistic interactions or attacks. Under these conditions, we expected that infants at Isla Brasilera would make more contact with their mothers and thereby reduce their risk from solitary males or extragroup individuals. We also expected that mothers at Isla Brasilera would be more protective than mothers at San Cayetano. However, our findings indicated that even though Isla Brasilera's infants made more contact with their mothers, mothers did not reject less nor did they break contact less frequently with their infants compared to San Cayetano. It is possible that the demographic situation of Isla Brasilera favors mothers who are less willing to care for their offspring because they are actively participating in intergroup encounters, situations that promote the exchange of social/reproductive information between neighboring groups [Kowalewski and Garber, 2010].

We conclude that in general, the patterns of mother-offspring conflict are generally consistent across the two study sites despite differences in the

demographic and social features of the two populations. It is important to note that mother-offspring conflict is a dynamic process and therefore is likely influenced by multiple factors that vary over time and across social and demographic landscapes. Other factors that must be considered in future studies of mother-offspring conflict include the nutritional requirements of mothers, especially during lactation and conception of new infants, the effect of certain diseases (for example the presence of intestinal parasites can decrease the fat concentration of milk) [Hinde, 2007], social traits (differential maternal investment based on infant sex, sexual activity of the mother, birth of siblings, changes in the composition of groups, replacement of adult males), and life-history variables (condition of the mother and maternal age). Finally, this study suggests that the environmental variability (ecological, demographic, and social traits) may lead to a set of strategies used both by infants and mothers with the main goal of conflict resolution and specifically to mothers to cope with a tradeoff between current and future reproduction.

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