

Preliminary study of mother–offspring conflict in black and gold howler monkeys (*Alouatta caraya*)

Romina Pavé · Martin M. Kowalewski ·
Silvana M. Peker · Gabriel E. Zunino

Received: 8 May 2009 / Accepted: 19 January 2010
© Japan Monkey Centre and Springer 2010

Abstract Parent–offspring conflict has been scarcely studied in Neotropical primates. In this study, we explored mother–offspring conflict in a group of wild black and gold howler monkeys (*Alouatta caraya*) in northeastern Argentina. We used the all-occurrences technique to record behaviors, completing 712 h of observation. The results showed that all immature individuals between 2 and 23 months expressed conflict with regard to suckling or traveling with their mothers. Successful suckling attempts negatively correlated with the age of the immatures, occurring least frequently with the presence of newborns. In the juvenile period, the decline in successful attempts was a consequence of juveniles reducing suckling attempts and mother rejection.

Keywords *Alouatta caraya* · Parent–offspring conflict · Mother–infant interactions · Nursing

Introduction

Parent–offspring conflict (POC) theory states that behavioral conflict in primates is a result of offspring demanding more parental investment (PI) than parents are selected to give (Trivers 1974). The cost of PI in a current infant will result in reduction of the parent’s ability to invest in future

offspring (Trivers 1972). Infant demands include a longer duration of parental care during young dependence and a longer investment period.

Behavioral conflicts between parents and offspring have been observed in non-human primates in several contexts, including resting (Horr 1977), feeding (Altmann 1980), suckling and traveling (Horvat and Kraemer 1982), and mother’s resumption of mating (Gomendio 1991; Schino et al. 2001).

Information on POC for Neotropical monkeys is limited (Maestriperi 2002), i.e., captive *Callithrix jacchus* (Ingram 1977; Locke-Haydon and Chalmers 1983). Although parent–offspring conflict has not been examined in howler monkeys per se, there are studies that have focused on infants which include some of the POC behaviors discussed here (*A. caraya*: Calegario-Marques and Bicca-Marques 1993a; *A. guariba clamitans*: Biedzicki de Marques and Ades 2000; Miranda et al. 2005; *A. palliata*: Clarke and Glander 1981; Clarke 1990; Clarke et al. 1998; *A. pigra*: Treves et al. 2003; *A. seniculus*: Agoramorthy and Rudran 1992; Rumiz 1992). *Alouatta caraya* is a folivore–frugivore arboreal Neotropical primate, sexually dichromatic and dimorphic, characterized by bisexual dispersal (Di Fiore and Campbell 2007). In this species the period of pregnancy is about 6 months, the average IBI is 16 ± 3.73 months ($N = 30$) if infants survive the first year of life, and the weaning period is from 9 to 12 months (Crockett and Eisenberg 1987; Rumiz 1990; Calegario-Marques and Bicca-Marques 1993b; Kowalewski and Zunino 2004).

The objective of this study was to explore behavioral conflict between mothers and immatures in black and gold howler monkeys (*A. caraya*). We also examined the effect of mother activity, pregnancy, and infant age in the mother–infant interaction.

R. Pavé (✉) · M. M. Kowalewski · S. M. Peker · G. E. Zunino
Estación Biológica Corrientes-Museo Argentino
de Ciencias Naturales, Av. Angel Gallardo 470,
C1405DJR Buenos Aires, Argentina
e-mail: rominaepave@yahoo.com.ar

M. M. Kowalewski
University of Illinois at Urbana-Champaign,
Champaign, IL, USA

Table 1 Age and demographic characteristics of individuals observed. IBI include only the birth of infants who survived to the subsequent pregnancy of their mothers

Individuals	Age (months) of study	Month and year of birth	Sex	Mother and IBI
Luca	0–4	May 2006	Male	Josefa (IBI: not available)
Charlie	0–11	October 2005	Female	Gorda (IBI = 12; $n = 1$)
Ema	5–16	May 2005	Female	Ana (IBI = 15.5; range = 14–17; $n = 2$)
Kaya	18–29	April 2004	Female	Ana
Fito	18–29		Male	Josefa

Methods

We conducted the study in a flooded forest on Isla Brasilera (27°18'S, 58°38'W) located near the confluence of the Paraná and Paraguay rivers in northeastern Argentina (Kowalewski and Zunino 2004). The availability of food (leaves, flowers, and fruits) is relatively constant throughout the year (Zunino et al. 2001; Kowalewski 2007). Births also occur throughout the year, supporting the hypothesis that howler monkeys do not have a fixed birth season at this site (Kowalewski and Zunino 2004).

We present data obtained during 5 consecutive days from sunrise to sunset each month from October 2005 through September 2006, a total of 712 h of observation. The study group was composed of 2 adult males, 3 adult multiparous females, 2 juveniles (1 female, 1 male), 3 infants (2 females, 1 male; 2 born during this study), and 2 newborns born in the last month of the study. In Table 1 we present data on each of the 5 immatures studied (3 infants, 2 juveniles). Individuals were recognized by body size, pelage colors, scars, and artificial marks (ear tags and colored anklets). We considered an infant to be from birth to 1 year old, and a juvenile to be between 1 and 3 years for females, and 1 to 4 years for males (Rumiz 1990). During the first month of life, infants were with their mothers 100% of the time (mainly in ventral contact) making it impossible to observe all the infant attempts at suckling. From January 2006 to the end of the study, we registered systematic suckling attempts (accepted or rejected) of infants, from 30 days of life, towards their mothers.

We used the all-occurrences technique (Altmann 1974) to record the behavior of infants, juveniles, and their mothers. This technique was also used to record the mating behavior of the mothers. Recorded behaviors fulfilled the conditions for the application of this sampling technique (Altmann 1974): all behaviors were “attention-attracting”, behavioral events were easy to record, and we studied a small number of known individuals. Three observers recorded the behaviors, thus when the group divided into 2 or 3 subgroups they were followed simultaneously. Table 2 describes the variables analyzed. Maternal rejection of suckling was expressed as the relative frequency of rejection (dividing the frequency of rejections by the frequency

Table 2 Behavioral variables analyzed

Behaviors	Description
Suckling attempts	The infant touches the body of its mother, whimpers and tries to gain access to the nipple, moving its mouth to the nipple
Suckle	The infant has oral contact with the nipple of its mother. Infant may or may not be involved in active nursing (from Bentley-Condit 2003)
Rejection	The mother prevents the infant from climbing or gaining access to the nipple. Patterns of rejection of climbing include: pushing the infant away (when the infant attempts to climb), removing the infant (when the infant is over the mother's body). Patterns of rejection of suckling include: moving away, pushing the infant away, obstructing access to the nipple with an arm, resting with inaccessible nipples, and distracting groom
Distress calls	The infant gives loud vocalizations in response to mother rejection
Tantrums	Include jerking, screaming, and biting the mother
Following the mother	The infant pursues the mother when she moves away. Infant may or may not give distress calls

of total infant attempts). This variable was utilized in other studies of POC in primates (Locke-Haydon and Chalmers 1983; Hauser and Fairbanks 1988; Gomendio 1991; Schino et al. 2001). We calculated monthly averages as the unit of analysis when using Spearman's rank correlation tests following Zhao et al. (2008). Statistical significance was set at $\alpha < 0.05$.

Results

Changes in suckling

We observed 247 attempts of immatures to suckle their mothers, 218 attempts were accepted and 29 rejected. During the first 12 months, suckling attempts correlated negatively with infant age ($r_s = -0.71$, $n = 12$, $P = 0.009$). The accepted suckling attempts also correlated negatively with infant age ($r_s = -0.80$, $n = 12$, $P = 0.002$). We describe the changes for each infant below.

Mothers accepted nursing of the 3 infants during resting, feeding, traveling, howling, allogrooming, grooming the same immature, and defecation. Two mothers allowed their infants to suckle when they were feeding and one mother while traveling until the infants were 3 months. The oldest immature that suckled was 15 months.

Two of the 3 mothers (Ana and Gorda) mated with resident males of the group while they had infants between the ages of 4 and 15 months. We observed 13 copulatory bouts for Ana (months 7–15 of Ema) and 17 for Gorda (months 4–9 of Charlie). On average, there was a coincidence of 68.5% (range 57.1–80%) between the occurrence of copulatory bouts and maternal rejection during the same month. On 4 occasions that infants were less than 1 m from their mothers they did not attempt to harass or physically interpose themselves between the mating adults.

Conflict with mother

Maternal rejection of suckling increased as immatures grew older. Because of the low frequency of maternal rejection, it was not possible to conduct statistical analysis for comparison between ages. We described the changes for each infant below. With regard to the juveniles, all 5 suckling attempts were rejected by mothers. The longest conflict of suckling lasted up to 23 months with a juvenile female (Kaya) whose mother had a newborn (Ema).

Mothers rejected immature suckling attempts when they were feeding, giving milk to another infant (sibling or not sibling), and resting. Maternal rejection included: moving away (observed 11 times), pushing the infant away (8 times), distracting the infant through grooming (3 times), obstructing access to the nipple with an arm (2 times), mother showing teeth (once), and mother resting in a way that nipples were inaccessible (once). Immature responses to rejections included: giving distress calls and having tantrums, following the mother and resting next to her, and/or moving away to eat solid food. In 2 cases, an older infant female (Charlie, 11 months) bit the shoulder of her mother after maternal rejection of suckling (the mother had given birth to a new infant the previous day).

Mothers left infants behind after 3–4 months ($N = 2$). After month 4 ($N = 2$), infants began to follow the group independently. Although they were carried after giving loud cries, mothers stopped carrying them after month 7 ($N = 2$). Maternal rejection of infant carrying was recorded on 5 occasions in 1 mother–offspring dyad (Gorda–Charlie) when the infant was between 4 and 6 months. Mother rejection behaviors included: pushing the infant

away ($N = 1$ record) and removing the infant ($N = 4$ records).

Individual changes in suckling

Infant 1: Luca (month 0–4)

The highest frequency of attempts occurred at month 3 and declined 47.8% during months 3 and 4. The frequency of accepted attempts by the mother was similar to the

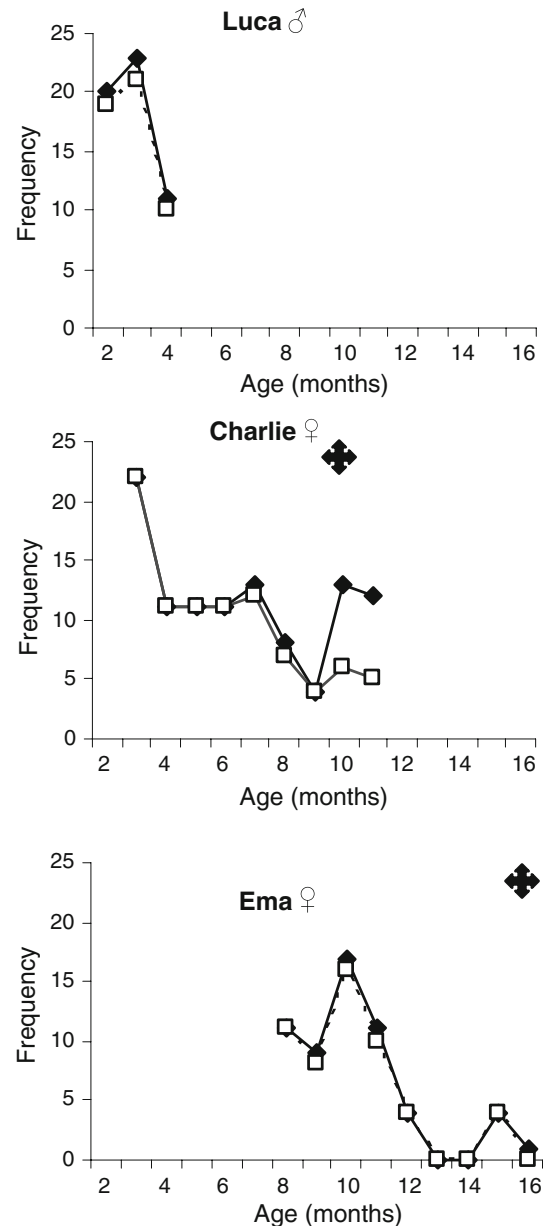


Fig. 1 Frequency of suckling attempts by each infant and accepted attempts by the mothers for each infant. Suckling attempts filled diamonds, accepted attempts of suckling open squares, birth is denoted by ◆

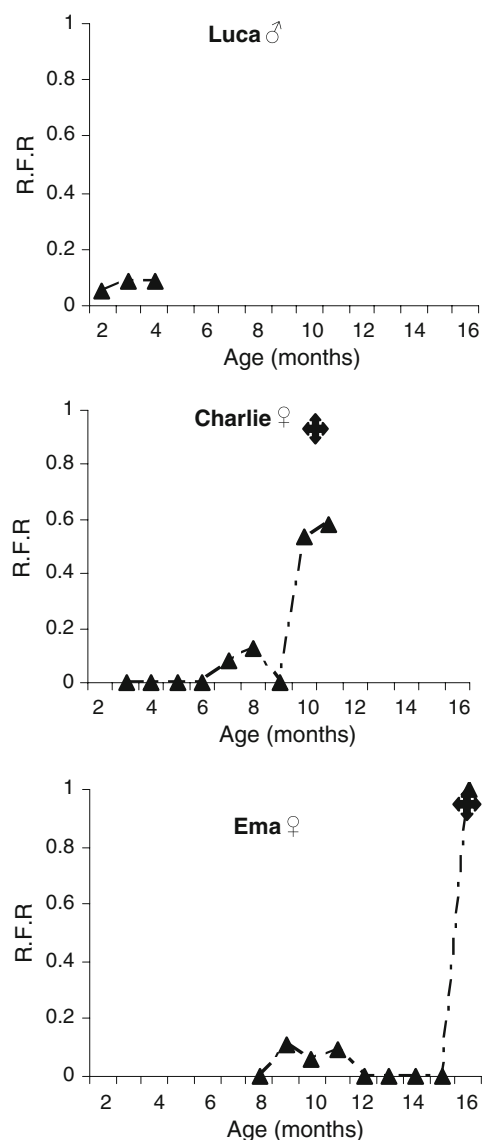


Fig. 2 Relative frequency of rejection (RFR) of suckling attempts by infants. Birth is denoted by ◆

attempts made by the infant (Fig. 1). Maternal rejection began at month 2; this age corresponded to the youngest age in which a mother rejected an infant attempt at suckling (Fig. 2).

Infant 2: Charlie (month 3–11)

The highest frequency of attempts occurred at month 3 and declined 50% between months 3 and 4. At month 9, the mother accepted all infant attempts and from months 10 to 11 both infant attempts and maternal rejection increased (Figs. 1 and 2). This coincided with the last months of pregnancy and the birth of a newborn. After the birth of the newborn, the mother rejected all infant suckling attempts.

Infant 3: Ema (month 8–16)

The highest frequency of attempts occurred at month 10 and coincided with the first month of pregnancy of the mother. The attempts at month 15 coincided with the last month of pregnancy, and they were all accepted (Fig. 1). After the birth of the newborn, the mother rejected all suckling attempts of Ema (Fig. 2).

Discussion

Changes in suckling

Infants' suckling attempts lasted up to 23 months of age; however, mothers nursed their offspring only up to 15 months. Possibly because of an increase of milk availability during new pregnancies or with newborns in mothers of immatures of 10–15 months, the suckling attempts increased and the immatures had access to the nipple. Clarke (1990) also observed that mothers continued to nurse their offspring into early pregnancy in *A. palliata*. These observations support a prediction derived from the POC theory (Trivers 1974): offspring demand investment from their parents even at expenses of their siblings. However, the costs associated with milk sharing remain unknown. Mothers mated while they were nursing their offspring between months 4 and 15. These copulations coincided with maternal rejection of infant suckling attempts during the same month. Similar results were obtained in *Macaca fuscata* (Worlein et al. 1988), *M. mulatta* (Gomendio 1991; Berman et al. 1993; Schino et al. 2001), *Papio cynocephalus* (DeVore 1963), and *Trachypithecus leucocephalus* (Zhao et al. 2008).

Conflict with mother

As the highest proportion of suckling attempts was accepted, we observed a low frequency of maternal rejection to all the immatures. The youngest age at which we observed a suckling conflict was 2 months and the mother of the infant (Luca) was resting. In Clarke's (1990) study, mothers of *A. palliata* began to reject the infant suckling attempts after week 7 in the context of feeding and after month 3 when the mother traveled. Our results similarly show that even during resting, *A. caraya* mothers begin to reject their offspring at young ages. Nursing stopped when mothers had newborns. Several studies in non-human primates have reported that maternal care decreases after a sibling's birth and that weaning is also completed at this time (Tanaka 1992; Schino and Troisi 2001; DeVinney et al. 2003). In contrast, Rumiz (1992) observed that young juveniles of *A. seniculus* continued suckling after the birth

of younger siblings. In this study, juveniles continued trying to suckle until 23 months after the birth of new siblings but mothers rejected all the suckling attempts. Maternal rejections of suckling were not aggressive in *A. caraya*, and the patterns observed have been reported in other primates (i.e.: *A. palliata*: Clarke 1990; *M. fuscata*: Schino et al. 2001; *M. mulatta*: Gomendio 1991; *P. cynocephalus*: Altmann 1980). Immature individuals used both passive and aggressive responses against the maternal rejection of suckling. In this regard, Rumiz (1992) reported that older infants of *A. seniculus* harassed their mothers after maternal rejection. Mothers began to leave behind the infants at 12–16 weeks. This seems to be later than the 6 week (male) and 7 week (females) reported by Clarke (1990) for *A. palliata*. Mothers transported infants after they gave loud cries until 7 months. It is possible that mothers interpreted loud cries as honest signals of need (but see Hauser 1986); therefore, they responded by helping their offspring. This last observation is consistent with a prediction of POC theory (Trivers 1974): infants emit distress calls at a higher frequency than necessary; therefore, mothers may use both age and call intensity as reliable cues to respond to infant solicitations (Altmann 1980; Bateson 1994).

Despite the limitations of our data, the results obtained support some predictions of the POC theory in wild *A. caraya*. However, more studies are needed to understand the evolution of mother–infant relationships in howler monkeys.

Acknowledgments We thank the Centro de Capacitación Comunitaria of Isla Cerrito for logistic support. We are very grateful to all field assistants that helped us in data collection. We thank Melissa Raguét for valuable comments on an earlier version of this manuscript. This study was supported by the National Council of Research and Technology of Argentina (CONICET) (S.P.) and the American Society of Primatology (S.P.).

References

- Agoramoorthy G, Rudran R (1992) Adoption in free-ranging red howler monkeys, *Alouatta seniculus* of Venezuela. *Primates* 33:551–555
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge
- Bateson P (1994) The dynamics of parent–offspring relationships in mammals. *Trends Ecol Evol* 9:399–402
- Bentley-Condit VK (2003) Sex differences in captive olive baboon behavior during the first fourteen days of life. *Int J Primatol* 24:1093–1112
- Berman CM, Rasmussen KLR, Suomi SJ (1993) Reproductive consequences of maternal care patterns during estrus among free-ranging rhesus monkeys. *Behav Ecol Sociobiol* 32:391–399
- Biedzicki de Marques AA, Ades C (2000) Male care in a group of wild *Alouatta fusca clamitans* in Southern Brazil. *Folia Primatol* 71:409–412
- Calegario-Marques C, Bicca-Marques JC (1993a) Allomaternal care in the black howler monkey (*Alouatta caraya*). *Folia Primatol* 61:104–109
- Calegario-Marques C, Bicca-Marques JC (1993b) Reprodução de *Alouatta caraya* Humboldt, 1812 (Primates, Cebidae). *A Primatologia do Brasil* 4:51–66
- Clarke MR (1990) Behavioral development and socialization of infants in a free ranging group of howling monkeys (*Alouatta palliata*). *Folia Primatol* 54:1–15
- Clarke MR, Glander KE (1981) Adoption of infant howling monkeys (*Alouatta palliata*). *Am J Primatol* 1:469–472
- Clarke MR, Glander KE, Zucker EL (1998) Infant–nonmother interactions of mantled howler infants with group members. *Int J Primatol* 19:451–472
- Crockett CM, Eisenberg JF (1987) Howlers: variations in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wingham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 54–68
- Devinney BJ, Berman CM, Rasmussen KLR (2003) Individual differences in response to sibling birth among free-ranging yearling rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Behaviour* 140:899–924
- DeVore I (1963) Mother–infant relations in free-ranging baboons. In: Rheingold HL (ed) *Maternal behavior in mammals*. Wiley, New York, pp 305–335
- Di Fiore A, Campbell CJ (2007) The Atelines: variation in ecology, behavior, and social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) *Primates in perspective*. Oxford University Press, New York, pp 155–185
- Gomendio M (1991) Parent/offspring conflict and maternal investment in rhesus macaques. *Anim Behav* 42:993–1005
- Hauser MD (1986) Parent–offspring conflict: care elicitation behaviour and the “cry-wolf” syndrome. In: Else JG, Lee PC (eds) *Primate ontogeny, cognition, and social behaviour*. Cambridge University Press, Cambridge, pp 193–203
- Hauser MD, Fairbanks LA (1988) Mother–offspring conflict in vervet monkeys: variation in response to ecological conditions. *Anim Behav* 36:802–813
- Horr DA (1977) Orangutan maturation: growing up in a female world. In: Chevalier-Skolnikoff S, Poirier FE (eds) *Primate bio-social development*. Garland, New York, pp 289–321
- Horvat JR, Kraemer HC (1982) Behavioral changes during weaning in captive chimpanzees. *Primates* 23:488–499
- Ingram JC (1977) Interactions between parents and infants and the development of independence in the common marmoset (*Callithrix jacchus*). *Anim Behav* 25:811–827
- Kowalewski MM (2007) Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. PhD thesis, University of Illinois at Urbana-Champaign
- Kowalewski MM, Zunino GE (2004) Birth seasonality in *Alouatta caraya* in northern Argentina. *Int J Primatol* 25:383–400
- Locke-Haydon J, Chalmers NR (1983) The development of infant–caregiver relationships in captive common marmosets (*Callithrix jacchus*). *Int J Primatol* 4:63–81
- Maestripieri D (2002) Parent–offspring conflict in primates. *Int J Primatol* 23:923–951
- Miranda JMD, Aguiar LM, Ludwig G, Moro-Rios RF, Passos FC (2005) The first seven months on an infant of *Alouatta guariba* (Humboldt) (Primates, Atelidae): interactions and the development of behavioral patterns. *Rev Bras Zool* 22:1191–1195
- Rumiz DI (1990) *Alouatta caraya*: population density and demography in Northern Argentina. *Am J Primatol* 21:279–294
- Rumiz DI (1992) Effects of demography, kinship, and ecology on the behavior of the red howler monkey, *Alouatta seniculus*. PhD thesis. University of Florida

- Schino G, Troisi A (2001) Relationship with the mother modulates the response of yearling Japanese macaques (*Macaca fuscata*) to the birth of a sibling. *J Comp Psychol* 115:392–396
- Schino G, Majolo B, Ventura R, Troisi A (2001) Resumption of sexual activity affects mother–infant interactions in Japanese macaques. *Behaviour* 138:261–275
- Tanaka I (1992) Three phases of lactation in free-ranging Japanese macaques. *Anim Behav* 44:129–139
- Treves A, Drescher A, Snowdon CT (2003) Maternal watchfulness in black howler monkeys (*Alouatta pigra*). *Ethology* 109:135–146
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man 1871–1971*. Aldine, Chicago, pp 136–179
- Trivers RL (1974) Parent–offspring conflict. *Am Zool* 14:249–264
- Worlein JM, Eaton GG, Johnson DF, Glick BB (1988) Mating season effects on mother–infant conflict in Japanese macaques, *Macaca fuscata*. *Anim Behav* 36:1472–1481
- Zhao O, Tan CL, Pan W (2008) Weaning age, infant care, and behavioral development in *Trachypitecus leucocephalus*. *Int J Primatol* 29:583–591
- Zunino GE, González V, Kowalewski MM, Bravo SP (2001) *Alouatta caraya* relations among habitat density and social organization. *Primate Report* 61:37–46