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ORIGINAL ARTICLE

Sex differences in the behavior of wild *Alouatta caraya* infants

Romina Pavé[1] · Martín M. Kowalewski[2] · Gabriel E. Zunino[3] · Steven R. Leigh[4]

Abstract Several primates show sex-based differences in activity patterns and social interactions during infancy. These differences have been associated with adult social and reproductive functions of males and females and are related to male–male competition. Our goal was to describe behavioral patterns of wild *Alouatta caraya* male and female infants, a species with sexual dimorphism in body size and behavioral strategies during adulthood. We also examined the relationship between life history variables, infant sex and age, activity patterns, and social interactions in order to determine whether males and females follow different trajectories during early growth. Over a 27-month study, we observed 21 male infants and 14 female infants across two similar sites in northern Argentina. Data were analyzed using generalized linear mixed model (GLMM) tests. We found no differences in suckling time or weaning age between males and females (9.7 vs. 9.4 months), but male infants spent more time feeding on solid food and resting than female infants. Males also invested more time in contact with their mothers than did female infants, and mothers rejected and broke contact with males more frequently than with females. Other behavioral categories did not differ between the sexes. Our results suggest that higher nutritional demands of males compared with females may affect some behaviors. However, mothers of sons did not experience immediate trade-offs between current and future reproduction. Other behaviors, similarly expressed by the two sexes, suggest a similar developmental trajectory between male and female *A. caraya* infants, meaning that most differences emerge following the infant period.

Keywords Ontogeny · Sex differences · Behavioral strategies · Social relationships · Argentina

Introduction

During infancy, the period between birth and nutritional independence, individuals develop motor, manipulative, and social skills that allow them to survive and mature successfully in their adult life (Altmann 1980; Harvey and Clutton-Brock 1985). Several studies, mainly on African and Asian primates, have revealed sex-based differences in activity patterns and social behaviors throughout infancy. These differences have been associated with sexual dimorphism in adult body size and behavioral strategies related to social and reproductive functions of males and females, mainly as a consequence of male–male mating competition (DeVore 1963; Trivers 1974; Redondo et al. 1992; Leigh 1994; Plavcan 2001; Maestripieri and Ross 2004; Lonsdorf et al. 2014), dispersal patterns (Eaton et al. 1985; Clarke 1990; Nash 2003), and maternal social rank (Berman 1984; Rowell and Chism 1986; Gomendio 1990; Schino et al. 1999; Brown and Dixson 2000; Kulik et al. 2015). For example, Lonsdorf et al. (2014) found that wild male chimpanzees (*Pan troglodytes*) that are more gregarious and participate in more direct physical aggression

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than females during adulthood also invest more time in social play than females during infancy.

Sexual dimorphism in body size during adulthood may result in sex-based differences in somatic growth rates (i.e. weight gain), growth duration, or both through ontogeny (Leigh 1995). These differences may affect energy intake through milk or solid foods (depending on the age of infants for males and females; Trillmich 1986; Leigh 1994; Riek 2008).

Detailed studies on infant development in howlers and other atelines are scarce (*Alouatta caraya*: Pavé et al. 2010; *A. palliata*: Baldwin and Baldwin 1973; Whitehead 1986; Clarke 1990; Raguet-Schofield and Pavé 2015; *Brachyteles hypoxanthus*: Guimaraes and Strier 2001; Tolentino et al. 2008). The only comprehensive study of social behavior throughout the infant period in howler monkeys was carried out by Clarke (1990). She studied 11 infants from birth to 12 months and found that male and female *A. palliata* infants proceeded from birth along different trajectories of social development, corresponding with the types of sex-specific social interactions they would engage in as adults. For example, female infants reacted more positively than males to affiliative social interactions with other group members (4.5 vs. 1.1 reaction/h), and mothers rejected female infants less than male infants (0.4 vs. 0.9 rejection/h). However, it remains unclear how activity budgets and social life vary during infancy in other howler species.

We conducted our study on the black and gold howler monkey, *Alouatta caraya*, which exhibits sexual dimorphism in body size and behaviors (Di Fiore et al. 2011). *Alouatta caraya* mothers have similar inter-birth intervals (IBIs) following sons (14.23 ± 2.39 months, $N = 13$) and daughters (12.93 ± 1.77 months, $N = 15$; Pavé 2013). Although growth rates during infancy have been reported to be similar for males and females until they reach the age of 1 year (Leigh 1992a), these data are from captive animals, where food provisioning may accelerate growth rates, and do not reflect wild data on suckling and feeding time, intake rate, and food type acquired. After this period, males begin gaining weight much more rapidly than females, and age at growth cessation is 4.5 years for females and 7.5 years for males ($N = 27$ males, 26 females; Leigh 1992b, 1994). Adult males are 48 % heavier than adult females (6.42 ± 1.15 vs. 4.33 ± 0.76 kg; Rumiz 1990), and canine and hyoid size differs between sexes, with both structures reaching a larger size in males, and reflecting high male–male competition (Ford 1994; Gregorin 2006; Dunn et al. 2015; Van Belle and Bicca-Marques 2015). In addition, *A. caraya* exhibits sexual dichromatism, with males changing from a gold color during infancy to black in adulthood, while females are golden during all life stages (Bicca-Marques and Calegaro-Marques 1998).

Alouatta caraya live in uni-male–multi-female or multi-male–multi-female social groups that change their composition over time (Kowalewski 2007; Zunino et al. 2007; Pavé et al. 2012). The social groups typically host a central male (with higher mating success than the other resident males), while females have generally egalitarian relationships (Kowalewski and Garber 2010; Oklander et al. 2014). Male–male competition generates sex differences in adult behavioral strategies of howlers (Treves 2001; Kowalewski and Garber 2010; Oklander et al. 2014; Van Belle and Bicca-Marques 2015). *Alouatta caraya* females spend significantly more time than males in affiliative interactions such as grooming and care of infants. In contrast, males spend significantly more time in agonistic interactions such as howling and displays during intergroup encounters or fighting against extra-group males (Kowalewski et al. 1995; Kowalewski 2007; Holzmann et al. 2012). As in other howler species, both male and female *A. caraya* emigrate from their natal group, but female philopatry often occurs across populations (Calegaro-Marques and Bicca-Marques 1996; Kowalewski 2007; Oklander et al. 2010; Pavé unpublished data).

Given these species characteristics, black and gold howlers represent a good model for determining whether behavioral sex differences occur, and if so, how these differences emerge during ontogeny. There may also be differences between *A. caraya* and other well-studied primate species with regard to social life during infancy (cf. *Cercopithecus* spp.: Forster and Cords 2002; *Macaca* spp.: Eaton et al. 1985; Gomendio 1990; Schino et al. 1999; Brown and Dixson 2000; Maestripieri 2001; Kulik et al. 2015; *G. gorilla*: Maestripieri and Ross 2004; *P. troglodytes*: Boesch 1997; Lonsdorf et al. 2014). For example, bisexual dispersal prevails over philopatry, and there are no marked female dominance hierarchies in black and gold howler monkeys (Kowalewski 2007; Kowalewski and Garber 2010; Oklander et al. 2010).

Our goal, therefore, is to examine the activity and social patterns of wild *A. caraya* male and female infants throughout the first year of life in order to determine whether infant development is shaped by sexual dimorphism in body size and social life during adulthood. Based on published data, we propose the following hypotheses and predictions: (1) If *A. caraya* males have a faster growth rate than females during ontogeny (Leigh 1992a), we predict that (P1) male infants will invest more time in feeding and suckling than female infants throughout the infant period. (2) If, during adulthood, female *A. caraya* invest more time than males in affiliative interactions, and adult males invest more time than females in agonistic interactions (Kowalewski et al. 1995; Kowalewski 2007; Holzmann et al. 2012), we predict that (P2a) female infants will invest more time in affiliative social interactions and

time in mother-infant contact, and they will try to initiate contact with their mothers more frequently and will break contact less frequently than male infants; whereas (P2b) male infants will invest more time in playing-agonistic interactions and less time in affiliative social interactions and in mother–infant contact, and they will initiate contact with their mothers less frequently than female infants. These hypotheses and predictions are not mutually exclusive.

Methods

Study sites and subjects

Data were collected at two closely located sites in northern Argentina. One is an island named Isla Brasilera in Chaco Province (27°18′S, 58°38′W), and the other is a mainland site located in Parque Provincial San Cayetano and surrounding area (hereafter San Cayetano), Corrientes Province (27°30′S, 58°41′W). There is no substantial difference between sites in temperature, precipitation, or photoperiod (Rumiz 1990). The climate at both sites is subtropical, with a mean annual temperature of 21.6 °C and mean annual rainfall of 1200 mm (Servicio Meteorológico Nacional de Argentina). Isla Brasilera has an area of 292 hectares, characterized by continuous flooded forest located near the confluence of the Paraná and Paraguay rivers. At this site, births occur throughout the year (Kowalewski and Zunino 2004). Infant mortality at Isla Brasilera is 38 %, and the main known causes of infant deaths are attacks by adult males (8 %) and floods that affect the production of mature leaves (7.1 %) (Pavé et al. 2012). At San Cayetano, howlers live in fragments of semi-deciduous forest covering 224 hectares (Zunino et al. 2007). Births at this site are seasonal, occurring mainly between May and August (autumn–winter), and infant mortality is 35 %, caused mainly by male attacks (21 %) (Rumiz 1990; Zunino 1996). Howlers at the two study sites are similar in IBI, infant mortality rate, mother–infant relationship, and activity budget (Bravo and Sallenave 2003; Kowalewski 2007; Pavé et al. 2012, 2015).

We studied the behavior of 35 infants of known age—14 from five social groups on Isla Brasilera ($N = 4$ females and 10 males) and 21 from six social groups on San Cayetano ($N = 10$ females and 11 males)—over a period of 27 months (September 2008 to November 2010). Following Rumiz (1990), we defined the infant period from birth to 1 year of age. Infants were studied beginning in the month of birth ($N = 2$ infants from Isla Brasilera and 11 infants from San Cayetano) or in the months after birth ($N = 12$ infants from Isla Brasilera beginning between months 1 and 8, and $N = 10$ infants from San Cayetano beginning between months 1 and

6). In all cases, infants were studied until they reached 12 months of age or until their disappearance, confirmed death, or physical injury. All mothers were multiparous, identified by signs of previous nursing (elongated nipples). In all study groups there was some type of allomaternal care, i.e. transport, care/comfort, allosuckling, and allogrooming (Pavé 2013). Seven groups were uni-male-multi-female (1 adult male with 2–3 adult females) and four were multi-male-multi-female (2–3 adult males with 4–5 adult females). These groups ranged in size from 5 to 14 individuals. We identified individual howlers by age, sex, and natural and/or artificial markings (scars, color anklets, and ear tags). A more complete description of sites and howler groups can be found elsewhere (Pavé et al. 2012, 2015).

Data collection and analysis

We used focal animal sampling (Altmann 1974) to collect behavioral data on a monthly basis, assigning one full observation day per infant per month of life (between 0 and 11 months), from sunrise to dusk (from 6:20 to 19:30 in summer and 7:30 to 18:30 in winter). During focal samples, we continuously recorded all occurrences and durations of behavioral categories and interactions between the focal infant and all other group members (Table 1). In addition, we recorded data on mother–infant contact (i.e. time spent by the focal infant in physical contact with its mother, based on instantaneous point samples taken every 5 min during focal sampling).

The mutually exclusive behavioral categories used to characterize the activity patterns and social behaviors of infants (Table 1) were taken from previous studies (Hauser and Fairbanks 1988; Clarke 1990; Schino et al. 2001; Kowalewski 2007; Pavé et al. 2012, 2015). The frequency of making and breaking contact and of maternal rejection of suckling was analyzed between 2 and 11 months of age, because infants during the two first months of life (months 0 and 1) spend nearly all of their time in contact with their mothers. The weaning age corresponded to the last age of the infant in which we observed nipple contact with its mother (Borries et al. 2014). We collected a total of 2266 h of focal observation (680 h for Isla Brasilera and 1586 h for San Cayetano) and 27,208 instantaneous point samples (8127 points for Isla Brasilera and 19,081 for San Cayetano). These values average to approximately 10 h and 100 points per infant per month of life. We collected fewer data on Isla Brasilera because an extraordinary flood prevented us from visiting the study site between November 2009 and August 2010.

To analyze the effect of infant sex and age on the behavioral categories included, we used a generalized linear mixed model (GLMM) with a binomial error structure and logit-link function (Zuur et al. 2009). This analysis

Table 1 Behavioral categories used in this study and methods of recording

Behavior	Description	Recording method
Feeding	When the infant ingests and swallows solid food items or water	Focal sampling
Suckling	When the infant has oral contact with the nipple of its mother or another lactating adult female	Focal sampling
Potentially suckling (PS)	When the infant appears to have nipple contact with its mother or another lactating female but its face was not visible. PS represents around 70 % of the activity budget of infants in month 0 (Raguet-Schofield and Pavé 2015)	Focal sampling
Resting	When the infant is inactive, sitting or lying down, it can be sleeping or not	Focal sampling
Exploratory play	When the infant runs, jumps, and swings on branches and manipulates objects such as leaves and twigs	Focal sampling
Moving	When the infant moves independently within the same tree or between different trees	Focal sampling
Transport	When the infant is carried—in dorsal, ventral or lateral position—by its mother or another group member who is traveling	Focal sampling
Affiliative social interactions	When the infant is engaged in suckling attempts, interest (touch and sniff by other), care/comfort, grooming, and playing with its mother or another group member	Focal sampling
Agonistic social interactions	When the infant is engaged in fights, slaps, grabs, rejection, supplantations, and agonistic vocalizations with its mother or another individual	Focal sampling
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. The time in contact is independent of the activity of mothers and infants	Point samples
Mother makes contact (MMC)	When the mother initiates physical contact with the infant	Focal sampling
Mother breaks contact (MBC)	When the mother terminates physical contact with the infant	Focal sampling
Infant makes contact (IMC)	When the infant initiates physical contact with the mother	Focal sampling
Infant breaks contact (IBC)	When the infant terminates physical contact with the mother	Focal sampling
Absolute frequency of maternal rejection	All the instances in which mothers reject their offspring (i.e. in context of suckling, care/comfort, and transport) and when mothers finish a bout of suckling or transport	Focal sampling
Maternal rejection of suckling	This variable reflects the proportion of suckling attempts that mothers reject and was obtained by dividing the frequency of maternal rejections by the frequency of total suckling attempts	Focal sampling

controls for repeated measures on the same infant studied at different ages, incorporates both fixed and random effects, and allows analysis of proportions of time and rates (Bolker et al. 2009; Zuur et al. 2009). We calculated proportions and rates because each infant was represented by a different total number of hours of focal observation and instantaneous point sampling due to differences in observation time among seasons (10 h in winter, 11 h in spring and autumn, and 12 h in summer) and because infants were sometimes lost during observations. For these reasons, the time spent in each behavioral category, the frequency of making and breaking contact by mothers and infants, and the frequency of maternal rejection per infant per age were divided by the total time of the activity per infant per age. The same adjustment was made for the time in mother–infant contact obtained from point samples (see Pavé et al. 2015). In the models, the response variables were the proportion of time spent in mother–infant contact and in the behavioral categories studied, rates of making and breaking contact by mothers and infants, and rate of maternal rejection (these last behaviors are referred to as frequencies during the study; see Table 1). The predictor variables were both infant age and sex, and random factors were the identity of the infants nested within the groups and the group type (uni-male–multi-female or multi-male–multi-female) to which infants belonged nested within the sites. In addition to mean values, we also reported medians (and ranges) when summarizing <12 infants for age category or when there were outlying values. We considered $p \leq 0.05$ as the criterion for significance for statistical

tests. We performed statistical analyses using R version 3.0.3 with the MASS package.

Results

Activity patterns

The interaction between age and sex affected the time invested in suckling plus potentially suckling (suckling + PS), resting, exploratory play, and transport (Table 2). We also found sex differences in time invested in feeding, suckling + PS, and resting; in all these behaviors, male infants invested significantly more time than females (Table 2; Figs. 1, 2). Infant age significantly affected the time invested in feeding, suckling + PS, resting, exploratory play, moving, and transport (Table 2; Figs. 2, 3). The time invested in feeding, resting, and moving increased with infant age. In contrast, the time invested in suckling + PS, exploratory play, and transport decreased with infant age (Figs. 1, 2).

Feeding and suckling time

On average, male and female infants began to eat solid food items at the same age. However, the length of time was greater for males as a group than for females. At month 1 (week 5), 33.34 % of females ($n = 6$) and 37.5 % of males ($n = 8$) ate leaves and fruits. At month 2, however, 100 % of females ($n = 8$) and 62.5 % of males ($n = 8$) ate solid food. The remaining male infants began to eat solid food at month 3. Male infants invested more time in feeding than females, mainly between months 3 and 7 (Fig. 2). Males also invested more time than females in suckling + PS, mainly between months 5 and 11 (Fig. 2). Infants of both sexes were weaned at about the same average age, 9.7 ± 1.6 months for males (median = 10 month; range = 6–11 months; $n = 9$) and 9.4 ± 1.5 months for females (median = 9 months, range = 7–11 months, $n = 7$).

Resting time

Sex differences in resting time were more marked between months 1 and 5 (Fig. 1).

Exploratory play

Male and female infants spent similar lengths of time in exploratory play, with the highest activity levels between months 2 and 4 (Table 2; Fig. 1). During this period, infants began to move away from their mothers to explore the environment, after which the time invested in this

Table 2 Results from the GLMM for the effect of sex and age (months) of the infants (fixed factors) on the activity budget and social interactions

	$\beta \pm SE$	DF	t	p value
Feeding				
Intercept	-4.470 ± 0.212	184	-21.045	<0.001*
Age	0.325 ± 0.022	184	14.430	<0.001*
Sex (M > F)	0.623 ± 0.252	22	2.474	0.021*
Age*sex	-0.046 ± 0.028	184	-1.619	0.107
Variance of random factors = 0.199				
Suckling				
Intercept	-3.006 ± 0.219	184	-13.729	<0.001*
Age	-0.026 ± 0.032	184	-0.801	0.422
Sex	0.459 ± 0.292	22	1.570	0.162
Age*sex	-0.044 ± 0.043	184	-1.016	0.311
Variance of random factors = 0.287				
Suckling + potentially suckling				
Intercept	0.180 ± 0.181	184	0.995	0.321
Age	-0.313 ± 0.037	184	-8.319	<0.001*
Sex (M > F)	-0.571 ± 0.254	23	-2.251	0.034*
Age*sex	0.149 ± 0.048	184	3.135	0.002*
Variance of random factors = 3.38e−07				
Resting				
Intercept	-1.297 ± 0.124	184	-10.492	<0.001*
Age	0.104 ± 0.017	184	6.198	<0.001*
Sex (M > F)	0.348 ± 0.168	23	2.075	0.049*
Age*sex	-0.056 ± 0.022	184	-2.509	0.013*
Variance of random factors = 0.5179				
Exploratory play				
Intercept	-1.557 ± 0.213	184	-7.291	<0.001*
Age	-0.127 ± 0.031	184	-4.042	<0.001*
Sex	0.238 ± 0.295	23	0.807	0.427
Age*sex	-0.145 ± 0.048	184	-3.017	0.003*
Variance of random factors = 0.392				
Moving				
Intercept	-2.581 ± 0.178	184	-14.463	<0.001*
Age	0.132 ± 0.021	184	6.115	<0.001*
Sex	0.398 ± 0.227	23	1.752	0.089
Age*sex	-0.055 ± 0.029	184	-1.919	0.056
Variance of random factors = 0.244				
Transport				
Intercept	-1.794 ± 0.185	184	-9.673	<0.001*
Age	-0.299 ± 0.026	184	-11.368	<0.001*
Sex	0.319 ± 0.234	23	1.361	0.186
Age*sex	-0.147 ± 0.040	184	-3.645	<0.001*
Variance of random factors = 0.452				
Affiliative social interactions				
Intercept	-3.130 ± 0.240	184	-13.015	<0.001*
Age	-0.011 ± 0.033	184	-0.338	0.735
Sex	-0.029 ± 0.336	23	-0.086	0.932
Age*sex	-0.006 ± 0.046	184	-0.129	0.897
Variance of random factors = 0.361				
Agonistic social interactions				
Intercept	-4.376 ± 0.457	184	-9.568	<0.001*
Age	-0.043 ± 0.048	184	-0.906	0.366

Table 2 continued

	β ± SE	DF	t	p value
Sex	−0.115 ± 0.407	23	−0.283	0.779
Age*sex	0.089 ± 0.059	184	1.514	0.132
Variance of random factors = 0.423				
Time in mother–infant contact				
Intercept	2.457 ± 0.288	184	8.529	<0.001*
Age	−0.472 ± 0.042	184	−11.188	<0.001*
Sex (M > F)	−0.793 ± 0.360	23	−2.201	0.037*
Age*sex	0.171 ± 0.052	184	3.308	0.001*
Variance of random factors = 0.427				
Mother makes contact				
Intercept	−9.865 ± 0.377	162	−26.134	<0.001*
Age	−0.118 ± 0.054	162	−2.194	0.029*
Sex	0.270 ± 0.466	18	0.579	0.569
Age*sex	−0.019 ± 0.066	162	−0.298	0.766
Variance of random factors = 0.497				
Mother breaks contact				
Intercept	−9.023 ± 0.316	162	−28.518	<0.001*
Age	0.102 ± 0.038	162	2.682	0.008*
Sex (M > F)	1.333 ± 0.356	18	3.744	0.001*
Age*sex	−0.108 ± 0.044	162	−2.436	0.016*
Variance of random factors = 0.213				
Infant makes contact				
Intercept	−6.577 ± 0.169	162	−38.987	<0.001*
Age	−0.130 ± 0.024	162	−5.473	<0.001*
Sex	0.190 ± 0.214	18	0.888	0.386
Age*sex	0.008 ± 0.03	162	0.282	0.778
Variance of random factors = 0.25				
Infant breaks contact				
Intercept	−6.284 ± 0.186	162	−33.764	<0.001*
Age	−0.269 ± 0.029	162	−9.381	<0.001*
Sex	−0.172 ± 0.244	18	−0.707	0.489
Age*sex	−0.007 ± 0.039	162	−0.178	0.859
Variance of random factors = 0.27				
Absolute maternal rejection				
Intercept	−3.489 ± 0.298	184	−11.701	<0.001*
Age	0.127 ± 0.038	184	3.324	0.001*
Sex (M > F)	1.406 ± 0.361	23	3.897	<0.001*
Age*sex	−0.167 ± 0.048	184	−3.491	<0.001*
Variance of random factors = 0.23				
Maternal rejection of suckling				
Intercept	−4.641 ± 0.477	162	−9.727	<0.001*
Age	0.143 ± 0.057	162	2.505	0.0132*
Sex (M > F)	1.261 ± 0.566	18	2.227	0.0389*
Age*sex	−0.139 ± 0.070	162	−1.979	0.0495*
Variance of random factor = 0.25				

M males, F females

* Indicates statistically significant effect of a factor and/or interaction of factors in the model

activity gradually decreased. However, the significant interaction between sex and age suggests that as infants grew older, sex affected the time invested in exploratory

play, with females investing more time mainly during months 4 and 8 (Fig. 1).
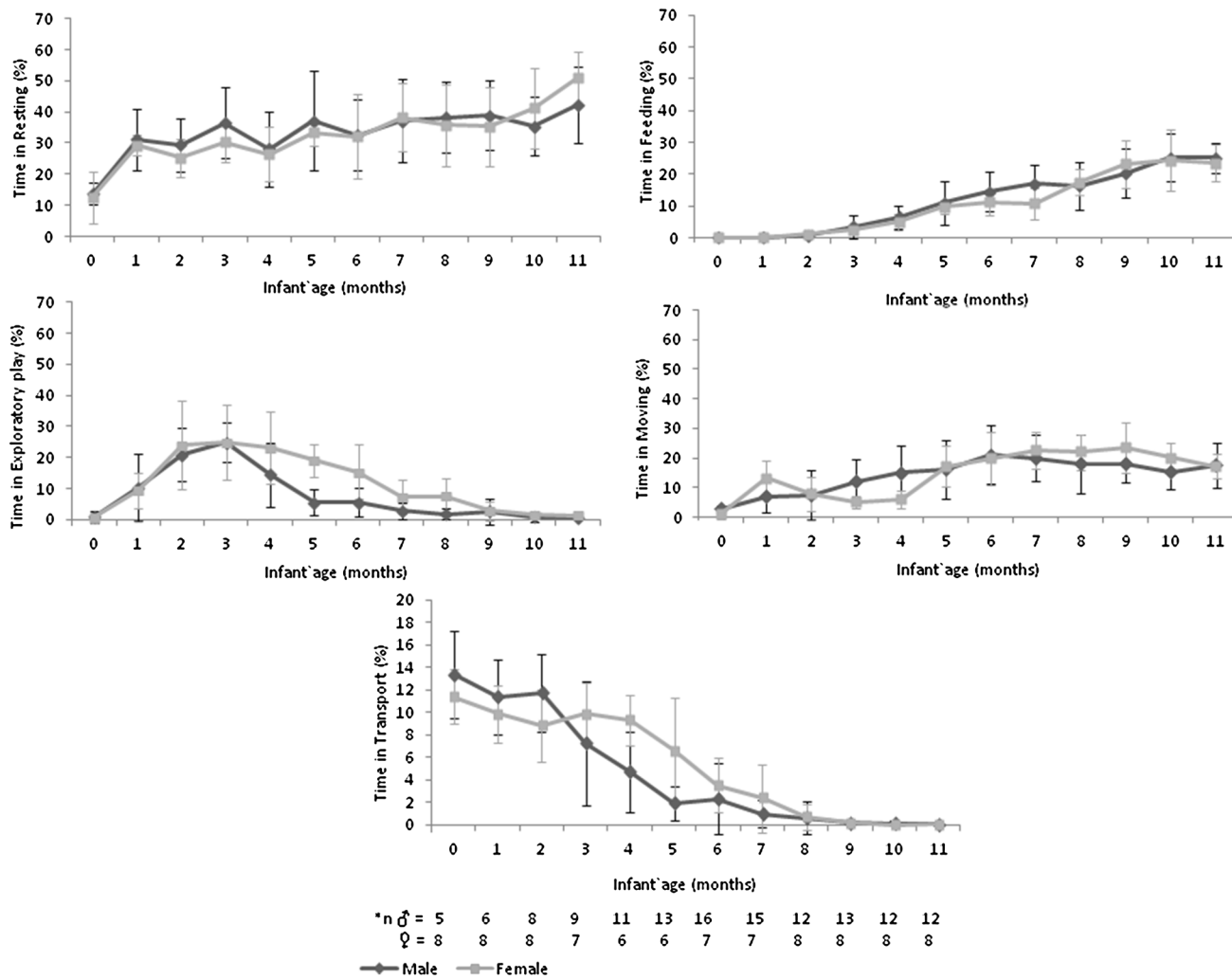
Moving and transport

With respect to moving, until month 2, both male and female infants moved independently a distance of 0.5–2 m within the same tree. Infants began to move alone from one tree to another and followed group displacements on their own by month 3 (Fig. 1). The time invested in transport by mothers and other group members was similar for male and female infants, although there was a significant interaction between age and sex, suggesting that sex affected the time invested in transport as infants grew older, with more transport of females than males (Table 2; Fig. 1). Nevertheless, infants of both sexes were transported until a similar age, 7.8 ± 2.4 months for males (median = 8 months, range = 3–11 months, $n = 12$) and 8.2 ± 1.6 months for females (median = 8.5 months, range = 6–11 months, $n = 8$). In general, the transport of old infants (>8 months) occurred mainly during group displacements in the context of intergroup encounters when the entire group moved rapidly.

Social interactions

The interaction between age and sex affected the time spent in mother–infant contact, mother breaking contact (MBC), absolute maternal rejection, and maternal rejection of suckling (Table 2). Also, infant sex alone was a significant predictor of time in mother–infant contact, MBC, absolute maternal rejection, and maternal rejection of suckling. Males spent significantly more time engaged in these three behavioral categories than did females (Table 2; Fig. 3). Infant age affected the time spent in mother–infant contact, mother making contact (MMC), MBC, infant making contact (IMC), infant breaking contact (IBC), absolute maternal rejection, and maternal rejection of suckling (Table 2; Fig. 3).

General social interactions

Affiliative and agonistic social interactions occurred at very low levels overall compared with the time spent in other activities. Additionally, as shown in Fig. 2, the time invested in affiliative interactions was higher than the time invested in agonistic interactions in both sexes throughout the infant period. Within affiliative interactions, we evaluated whether play on the one hand and care/comfort plus grooming of infants on the other hand differed qualitatively for male and female infants. However, we found no differences between males and females in either interaction, mainly because there was considerable variation among

Fig. 1 Mean proportion of time (in %) infants invested in resting, feeding, exploratory play, moving, and transport during the first 12 months of life by infant sex. The points represent the mean values (±SD) of all infants present by age. *n number of infants contributing to each age of the infant period by sex

males in play and among females in care/comfort plus grooming (Fig. 2).

Mother–infant relationship

For both sexes, mothers broke contact more than they made contact with their infants throughout the infant period, with the exception of month 2 (Fig. 3). In month 2, mothers of both sexes made contact more than they broke contact, mainly when they retrieved their infants from other group members, when infants were left behind during group displacements, and when infants moved away to explore the environment. Even though infant sex affected the frequency of MBC throughout the infant period, we observed a very similar pattern of MBC for the two sexes: the frequency of MBC increased until month 5 for males and month 7 for females, and then gradually decreased because infants made less contact with their mothers.

Infants of both sexes made contact with their mothers more frequently than they broke contact throughout the infant period, with the exception of month 2 (Fig. 3). At this age, infants began to move small distances (<1 m) away from their mothers to explore the environment and to interact with other group members. Both IMC and IBC gradually decreased after months 3 and 4 (during both months, infants had high levels of interaction with their mothers) for males and females. The decrease in these variables after month 5 suggests the beginning of infant independence.

Discussion

In this study, we examined activity patterns and social interactions throughout infancy among male and female *A. caraya*, and proposed differences in these variables between sexes as correlates of adult sexual dimorphism in
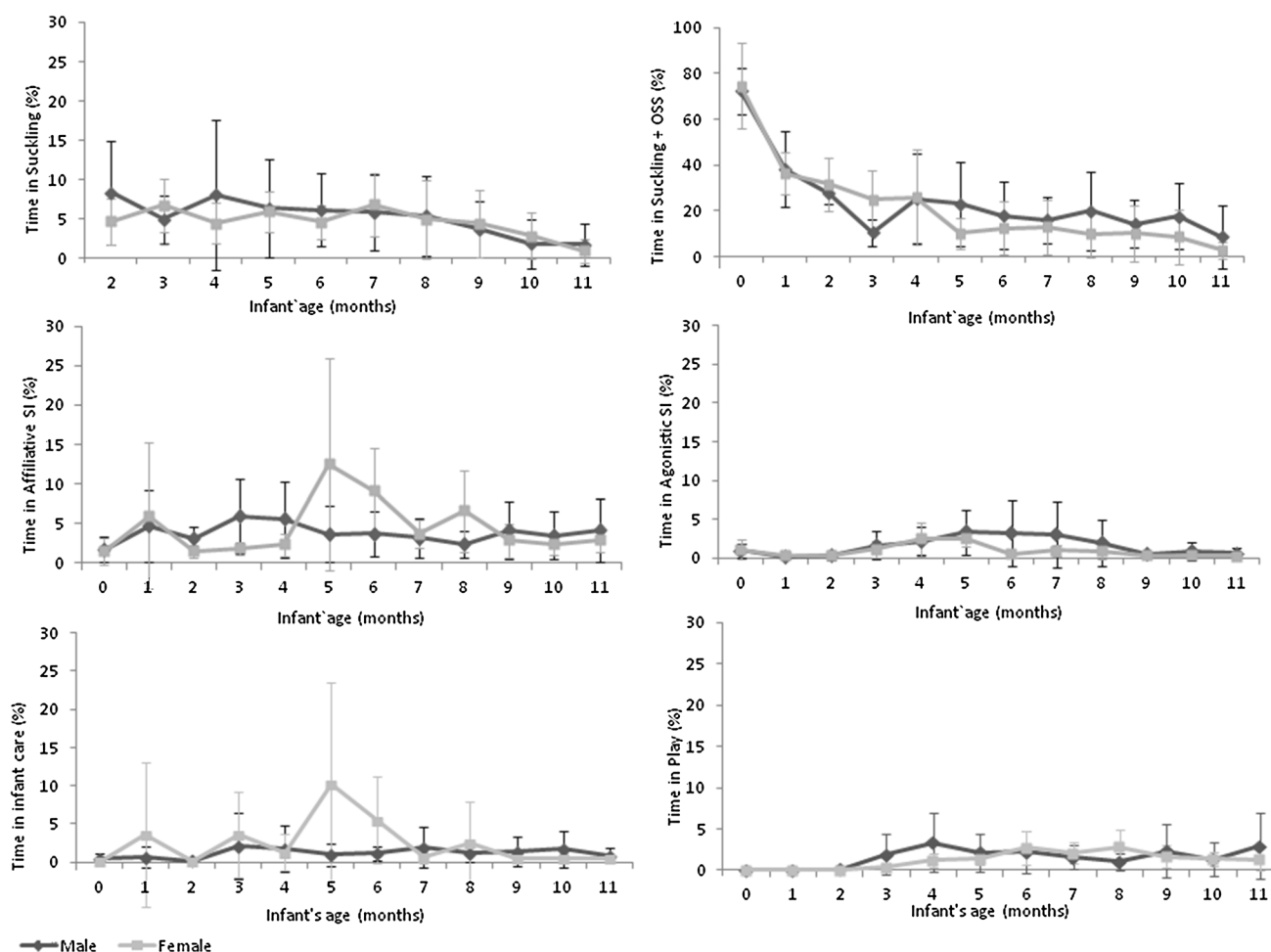
Fig. 2 Mean proportion of time (in %) infants invested in suckling, suckling + potentially suckling (PS), affiliative social interactions (SI), agonistic SI, infant care, and play during the first 12 months of life by infant sex. The *points* represent the mean values (±SD) of all infants present by age

body size and the different behavioral strategies used by adult male and female black and gold howlers. Results show considerable differences across the studied variables. As in other howler species (*A. guariba*, *A. palliata*, *A. seniculus*), infant age affected the time invested in several activities, suggesting that a general and gradual pattern of infant development exists for both sexes (Mack 1979; Clarke 1990; Kats and Otta 1991; Serio-Silva and Rodriguez-Luna 1994; Lyall 1996). *Alouatta caraya* infants had a prolonged mixed-feeding period (maternal milk plus solid food) that corresponded to approximately 81.82 % of the lactation period (between months 2 and 10). Combined with data on weaning age (around 9 months), the activity pattern indicates that *A. caraya* infants establish adult-like life as early as 8–9 months of age (Bicca-Marques and Calegaro-Marques 1994; Bravo and Sallenave 2003; Kowalewski 2007; Prates and Bicca-Marques 2008).

Sex differences between male and female black and gold howler infants were apparent in some, but not all, the behaviors we analyzed. For example, we found no sex differences in the time invested in suckling and in the weaning age. However, male infants spent more time feeding and suckling + PS than female infants (partially supporting P1). Overall, these results suggest that although maternal investment is similar for both males and females, including length of IBI, suckling time, and weaning age, males may have needed to consume more solid food throughout the infant period than females in order to deal with the energetic cost of a higher growth rate (Leigh 1994). Moreover, we cannot rule out the possibility that howler mothers may produce different volumes and composition of milk for each infant sex, as has been reported in *Macaca* spp. (Hinde 2007, 2009). Additionally, we consider that future research should integrate data for feeding time with data regarding the nutritional composition of foods consumed as well as foraging efficiency in order to obtain a more integrated perspective on feeding patterns during ontogeny.
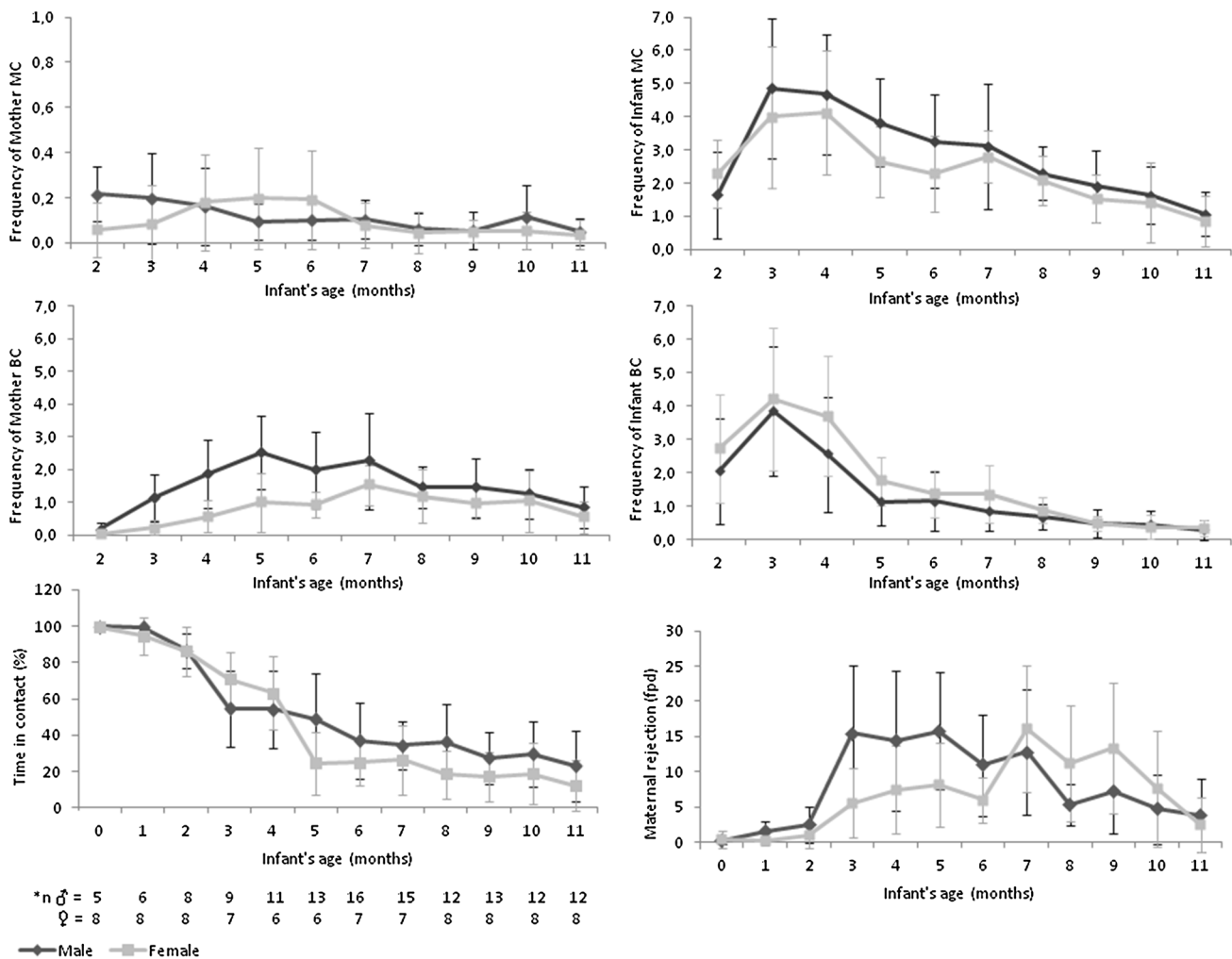
Fig. 3 Mean frequency per day (fpd) of observations of mothers making and breaking contact (MC and BC, respectively) with their infants and of infants MC and BC with their mothers, time in mother–infant contact by male and female infants, and mean fpd of observations of maternal rejection during the infant period. The *points* represent the mean values (±SD) of all infants present by age. *n number of infants contributing to each age of the infant period by sex

No sex differences were found in the time spent in exploratory play, independent moving, or transport. These results are consistent with findings among other primate species with sexual differences in body size and activity patterns during adulthood (exploratory play: *L. catta*, Gould 1990; *P. troglodytes*, Lonsdorf et al. 2014; *G. gorilla*, Maestripieri and Ross 2004; moving and transport: *L. catta*, Gould 1990; *M. fuscata*, Schino et al. 1999). However, our results, including the significant interactions between sex and age in exploratory play and transport, suggest that rates of both activities were higher for females than males. Although exploratory play is associated with the development of anti-predator strategies and food handling (Powell 2000), we found no differences between adult males and females in their participation in interactions with predators at our study sites (Fernández et al. in

revision). On the other hand, it is unlikely that adult females had better skills in food handling than adult males, as adults of both sexes have the same access to food. However, these aspects of the behavior of *A. caraya* have not been studied in detail with regard to sex differences during adulthood (but see Prates and Bicca-Marques 2008). With respect to transport, our results suggest a reduction in the transport of males as infants grew older, possibly because males were heavier than females at the same age. Similar to adult individuals, male and female infants did not differ in time invested in independent moving (Kowalewski 2007; Perez-Rueda et al. in revision). Additionally, sex differences were apparent in resting, with male infants spending more time than female infants. The greater time invested in resting by male infants may be a consequence of their higher feeding time compared with

female infants, i.e. high food consumption requires a high proportion of resting time devoted to the processing of food (Milton 1998).

In contrast to our predictions on social interactions, we found no sex differences in the time spent in affiliative or agonistic interactions (partially rejecting P2). Differences between sexes in these aspects of the social behavior of *A. caraya* may appear after the first year of life, during the last phases of juvenility, when hormonal activities change. This would be comparable to other primates with adult sex-based differences in social activities (e.g., *Chlorocebus pygerythrus*: Fairbanks 2002; *M. mulatta*: Kulik et al. 2015; *P. troglodytes*: Lonsdorf et al. 2014). Alternatively, the lack of sex differences in time spent in affiliative and agonistic social interactions among infants might be the result of a lack of sex-biased dispersal and a less pronounced dominance hierarchy among individuals in this primate species compared to other species whose infant development has been well studied (*M. fuscata*: Eaton et al. 1985; *M. mulatta*: Brown and Dixson 2000; *G. gorilla*: Maestripieri and Ross 2004). Nevertheless, this study suggests that, beginning in infancy, *A. caraya* individuals spend more time in affiliative than in agonistic interactions, and therefore, the pattern of social relationships that characterizes *A. caraya* societies (Kowalewski 2007; Oklander et al. 2014) develops early in ontogeny.

We found sex differences in the analyses of mother–infant relationships. First, male infants spent more time in mother–infant contact than female infants (partially rejecting P2). Although the same result was found in *M. fuscata* between high-ranking mothers and their sons (Schino et al. 1999), previous studies have generally shown that infant sex does not affect the time in mother–infant contact (*Erythrocebus patas*: Rowell and Chism 1986; *M. mulatta*: Brown and Dixson 2000; *L. catta*: Gould 1990; *G. gorilla*: Nowell and Fletcher 2007; *Galago senegalensis*: Nash 2003). Notwithstanding the need for further research on the nutritional traits of milk, we suggest that male infants may have spent more time in contact with their mothers because they were trying to acquire more milk from them. We found that mothers broke contact and rejected male infants more frequently than females (partially supporting P2). These results are consistent with previous studies including primate species with female philopatry (*M. fuscata*: Eaton et al. 1985) and bisexual dispersal (*A. palliata*: Clarke 1990). The other variables used to estimate parent–offspring conflict (MMC, IMC and IBC) did not differ between the infant sexes, supporting results from previous studies (*M. mulatta*: Brown and Dixson 2000; *Cercopithecus mitis*: Forster and Cords 2002; *L. catta*: Gould 1990). Overall, we failed to find a pattern of mother–infant relationship biased to one sex in *A. caraya*, possibly because, although this is a sexually

dimorphic species, no dominance hierarchy exists among individuals within groups, and dispersal patterns are variable (Kowalewski 2007; Kowalewski and Garber 2010; Oklander et al. 2010, 2014). The pattern recorded between mothers and male infants may reflect the high nutritional demands imposed by the male growth rate, and the denial of access to the nipple may be a product of the similar maternal investment in male and female infants by *A. caraya* mothers.

Overall, all the variables used to evaluate the mother–infant relationship, and specifically to estimate mother-offspring conflict (time in contact, MMC, MBC, IMC, IBC, and maternal rejection), varied significantly with infant age. These results coincide with those of previous studies (*C. mitis*: Forster and Cords 2002; *M. fuscata*: Eaton et al. 1985; *Trachypithecus leucocephalus*: Zhao et al. 2008; *P. cynocephalus*: Altmann 1980; *G. gorilla*: Nowell and Fletcher 2007; *L. catta*: Gould 1990). For example, as infants grow older, contact and proximity of the infant–mother dyad decline. All of these behavioral changes promote infant independence (Altmann 1980). This pattern of social development during ontogeny seems to be a conserved characteristic among non-human primates despite differences in social system, philopatry, and weaning age (Altmann 1980; Hauser and Fairbanks 1988; Clarke 1990; Gould 1990; Nowell and Fletcher 2007; Zhao et al. 2008; Pavé et al. 2015; Raguet-Schofield and Pavé 2015).

In conclusion, our study suggests that sex differences in *A. caraya* begin relatively early in ontogeny. Male howlers become larger than females by growing faster and slightly longer (Leigh 1992a, b). It is possible that their higher nutritional demands are revealed by feeding patterns during infancy, although analyses of nutritional ecology must be considered in future studies of infant development. However, this study shows that the age of weaning and termination of transport was similar in both sexes and also that neither IBIs nor the time spent in suckling was higher for male than for female infants. These results suggest similar trajectories and maternal investment in both infant sexes, and suggest that some social behavior traits of *A. caraya* in which we did not find sex differences might develop after the infant period, possibly during the juvenile period when hormonal activity increases (Stephens and Wallen 2013). Studies on infant development help advance the understanding of the variety of ontogenetic pathways found among non-human primates.

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