

Infant Development and Parental Care in Free-Ranging *Aotus azarai azarai* in Argentina

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Received February 23, 2004; accepted May 17, 2004

*Studies of infant development and parental behavior in free-ranging owl monkeys have been constrained by their nocturnal habits. Taking advantage of the cathemeral activity pattern of Aotus azarai azarai in the Argentinean Chaco, we describe the development of a cohort of free-ranging infants born in an owl monkey population in Formosa Province. We observed 7 infants, whose birth dates are known to the nearest week, to record details of their development and care between October 1999 and March 2000. We collected 92 h of behavioral data in 76 sessions. The infants were almost never off the parents during the first 4 wk of life, and we observed no infant being transported by a nonadult. The parent carrying the infant traveled most frequently in the middle of the group, sometimes first, but rarely last. The mean duration of 33 nursing episodes is 69 sec. After nursing, the infant was more likely to return to the nonnursing adult than to remain with the mother suggesting that in owl monkeys the infant may be primarily attached to the adult male in the group. Infants began to explore, to manipulate and to consume solid foods during the second month. Our observations are comparable to ones on captive breeding groups of Colombian owl monkeys (*Aotus lemurinus*) and Bolivian owl monkeys (*A. azarai boliviensis*) under controlled conditions of temperature, illumination and food availability.*

KEY WORDS: *Aotus*; monogamy; paternal care; development; infant carrying; infant foods.

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INTRODUCTION

In some primate species that live in socially monogamous groups, adult males exhibit paternal behavior and may carry the offspring for varying periods during early postnatal development (Snowdon, 1990). Examples include the marmosets and tamarins (Callitrichidae), titi monkeys (*Callicebus* spp.) and owl monkeys (*Aotus* spp.) of South America (Dixson and Fleming, 1981; Fragaszy, *et al.*, 1982; Mendoza and Mason, 1986a,b; Rotundo *et al.*, 2002; Tardif, *et al.*, 1992; Wright, 1984). Paternal care may be adaptive in promoting offspring survival or in offering increased foraging opportunities for the lactating female (Tardif, 1994). The mass of the developing infant represents a significant energetic investment for the parents, in addition to its nutritional demands.

The owl monkeys of Central and South America are represented by 2 major groups: grey-necked owl monkeys north of the Amazon River, and red-necked owl monkeys south of the river. The exact numbers of species is debated (Ford, 1994; Hershkovitz, 1983). The genus is widely distributed and all species live in small groups (Aquino and Encarnación, 1994; Fernandez-Duque *et al.*, 2001; Wright 1981). *Aotus* are unique among the Anthropoidea in having adapted to a nocturnal way of life (Wright, 1989).

The only detailed studies of parental behavior and infant development have been conducted on captive groups of owl monkeys (*Aotus azarai*) by Dixson and Fleming (1981), Jantschke *et al.*, (1996) and Wright, (1984). Parallel studies of infant development and parental behavior in free-ranging populations have been constrained by their nocturnal habits (Wright, 1985). However, in the Argentinean Chaco, (*Aotus azarai*) has a cathemeral activity pattern (Fernandez-Duque, 2003; Fernandez-Duque, *et al.*, 2001) and may be observed during daylight hours, as well as during the night. This fact, combined with their pronounced birth seasonality (Fernandez-Duque, *et al.*, 2002) has made it possible to accurately determine birth dates of infants and to observe their development in detail in the wild. We describe infant development during the first 5 postnatal mo for a cohort of 7 free-ranging *Aotus azarai* in Formosa Province, Argentina.

METHODS

Study Area and Population

We conducted the study in the eastern Chaco of Argentina, in a semi-deciduous gallery forest along the banks of the Pilagá River (58°11' W, 25°58' S) on lands belonging to the Estancia Guaycolec cattle ranch. The

study population consisted of 15 neighboring groups of *Aotus azarai azarai*, which have been subjects of regular observations since 1997 (Fernandez-Duque and Bravo, 1997). Group and individual densities in the area are 16 groups/km² and 64 individuals/km², respectively (Fernandez-Duque, *et al.*, 2001). Owl monkeys exhibit pronounced reproductive seasonality there: copulations occur from May to September, and births from late September to mid-December. Most births (>80%) are restricted to an 8-wk period (Fernandez-Duque *et al.*, 2002).

Data Collection

During the 1999 birth season, 3 observers monitored 12 social groups on a weekly basis to determine the occurrences of births (Fernandez-Duque *et al.*, 2002). Then for 5 mo we observed 7 infants whose birth dates were known to the nearest week, in order to record details of their development and care. The sex of the infants was unknown.

On each sampling day, we located a group before dawn and followed them until they went to sleep during the early morning. Thus the cessation of activity not the observer, determined the length of the observation session. We collected 92 h of behavioral data in 76 sessions that lasted on average 72 min (± 33 , range: 22 to 192 min). We collected behavioral data on the infant and the nearest adult uninterruptedly. It was only possible routinely to identify the male parent in one group. The numbers of monthly observation sessions achieved for the 7 infants are in Table I. Only one observer conducted the behavioral data collection.

We recorded the following measurements every 2 min: proximity of the infant to the nearest group member, position on its parents—dorsal, ventral, or ventrolateral, or resting in the flexure of the parent's thigh—and

Table I. Monthly number of observation sessions per infant

Infant	Month					Total observations per group
	1	2	3	4	5	
C0	2	2	2	1	2	9
D100	3	1	1	1	1	7
D1200	3	1				4
D500	1		2	1	2	6
D800	7	10	9	10		36
E500	1	4	1	3	1	10
F1200			2	1	1	4
Total observations per mo no. infants	17 6	18 5	17 6	17 6	7 5	76

activity: feeding, locomoting, resting. We scored occurrences of autogrooming and allogrooming once if they occurred during each 2-min interval. We recorded all occurrences of the following activities: infant gets off parent, infant moves away and returns to parent (an excursion), infant transfers from one parent to the other, suckling, play, food-sharing, and rates of travel, as measured by the frequency that they moved from one tree to another.

STATISTICAL ANALYSES

We present data recorded at 2-min intervals, i.e. instantaneous sampling, as percentage of number of sampling points. For example, if an infant were observed during 1 h, there would be 30 sampling points. If on 15 of the sampling points, we scored that the infant was off the parents, then we would say that it spent 50% of time off them. In other words, time and hours of activity refer to the number of 2-min sampling points. We analyzed data on behavioral categories recorded every time they occurred—all occurrences—as frequencies per h. We averaged data across each observation session and calculated means for each infant. The grand mean is the average across infants.

RESULTS

Time on and off Parents

The time an infant spent off the parents increased with age (Fig. 1). An infant was almost never off the parents during the first 4 wk of life. It spent >50% of time independently by the 3rd mo (65.2 ± 13.3 , $n = 6$ infants) and $\leq 90\%$ of time by the 4th mo (± 10.1 , $n = 6$). The positive and linear relationship between age and time off the parents is statistically significant ($\text{adj } R^2 = 0.873$, $F = 187.4$, $\text{df} = 27$, $p = 0.001$). We never observed an infant being transported by a non adult individual.

While the infant was on the parents, it regularly changed positions. During the first 2 wk, the infant was almost always positioned ventrally or ventrolaterally to the carrying adult (Table II). It began riding dorsally more frequently during the 3rd. By the 9th wk, most ventroventral contact between the infant and parent involved nursing episodes and the infant rode dorsally at other times.

Parents carried their infant most of the time during its first 2 mo, whenever they traveled between trees (98%). As the infant achieved locomotor independence, the percentage decreased to 63% during the 3rd mo and to

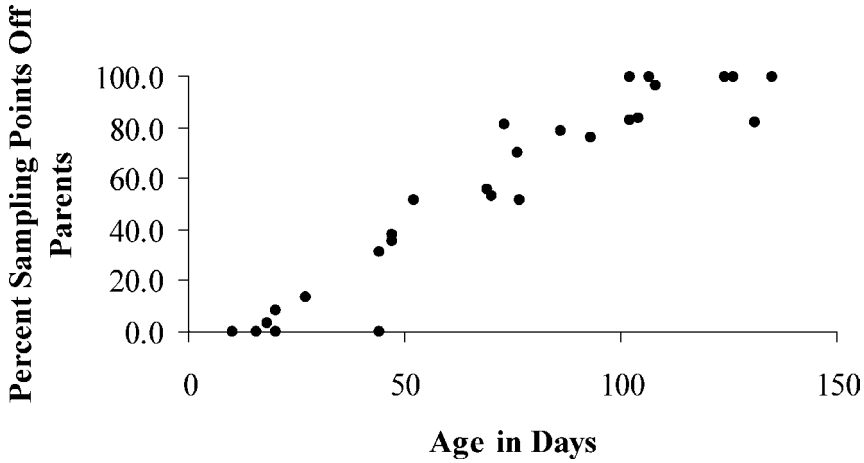


Fig. 1. Changes in the percent of sampling points infant was off the parents.

30% by the 4th mo. By the 5th mo, the parents seldom carried the infant when traveling (6%).

The parent carrying the infant traveled most frequently in the middle of the group, sometimes first, but rarely last (Fig. 2). The carrying adult traveled more frequently in the middle than first during the first mo of life of the infant (Wilcoxon $T = 15$, $z = -2.0226$, $p = 0.04$), whereas the differences are not statistically significant for the other months.

Table II. Percentage changes with age in the position adopted by the infant while on the parents

Age	VVL	D	n
Wk 1	94	6	4
Wk 2	98	2	3
Wk 3	45	55	2
Wk 4	32	68	4
Wk 5-8	13	87	5
Wk 9-12	3	97	6
Wk 13-16	5	95	5
Wk 17-20	0	100	5

Wk = week of life.
 VVL = ventral or ventrolateral.
 D = dorsal.
 N = number of infants observed.

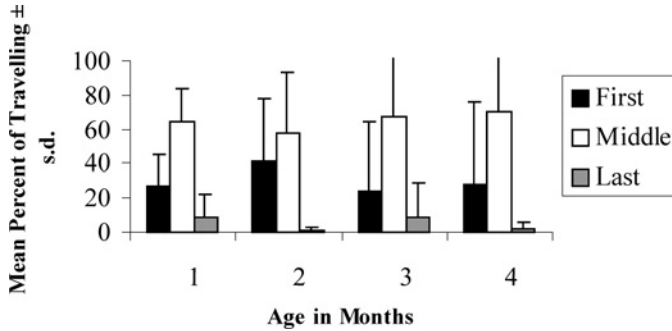


Fig. 2. Changes with age in the traveling position of parent carrying infant.

Locomotor Activity

During the 1st mo most locomotor activity consisted of the infant regularly changing positions on the carrier. It began to move by itself on the back of the male during the 3rd wk, but it was between the 4th and 6th wk it showed most activity on the back of the carrier. The increase in the level of activity is also reflected in the number of times the infant transferred from one parent's back to the other. The 9 occasions ($n = 3$ infants) when we observed infants transferring between parents occurred unassisted and while they were between 4 and 7 wk old.

As the infant matured, its locomotor activity increased. The frequency of infant excursions increased consistently from birth through the 3rd mo, then decreased (Fig. 3). After the 3rd mo the number of excursions decreased because the infant was independent most of the time.

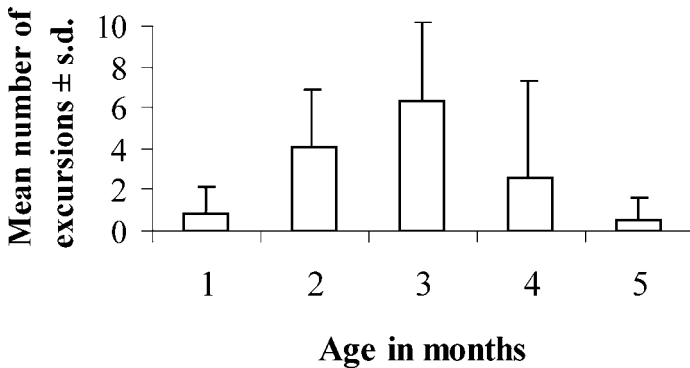


Fig. 3. Changes with age in the number of excursions of the infant.

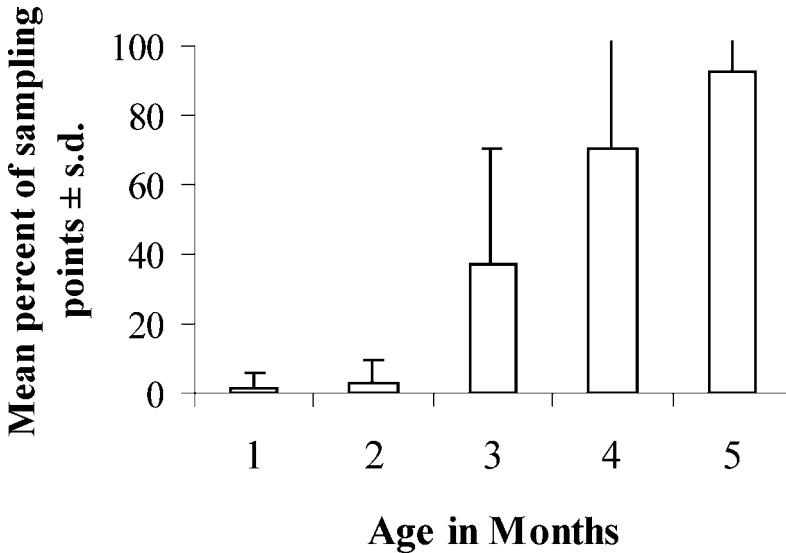


Fig. 4. Changes with age in the amount of independent travel.

As the infant achieved locomotor independence it began to travel alone. The amount of its travel independently between trees is highly correlated with age ($r = 0.829$, $p = 0.001$, $N = 28$, Fig. 4). Once again, it was during the 3rd mo that there was the major qualitative change. Then the infant traveled independently almost 40% of the time. By the end of the 5th mo, it seldom climbed on the back of a carrier to change trees as shown by the 92% value corresponding to the 5th mo.

The infant was never first when the group traveled. It moved in the middle of the group as much as last when it was 3 and 4 mo old (Wilcoxon tests, $p = 0.46$ and $p = 1$, Fig. 5). When it was older, i.e., 5th mo, it started to move last more frequently than in the middle. Then the difference is statistically significant (Wilcoxon test, $p = <0.05$).

The increase in the infant's locomotor activity is also reflected in changes in its proximity to other group members. During the first 2 mo the infant spent almost all the time ≤ 0.5 m of the nearest subject (Fig. 6). It spent *ca.* 80% of the time in physical contact with another individual. However, during the 3rd mo the infants began to spend more time away, with a significant increase in the time spent ≤ 3 or ≤ 5 m. By the 4th mo the infants spent most time ≤ 3 m of other group members, but they could be as far as 10 m from the nearest individual.

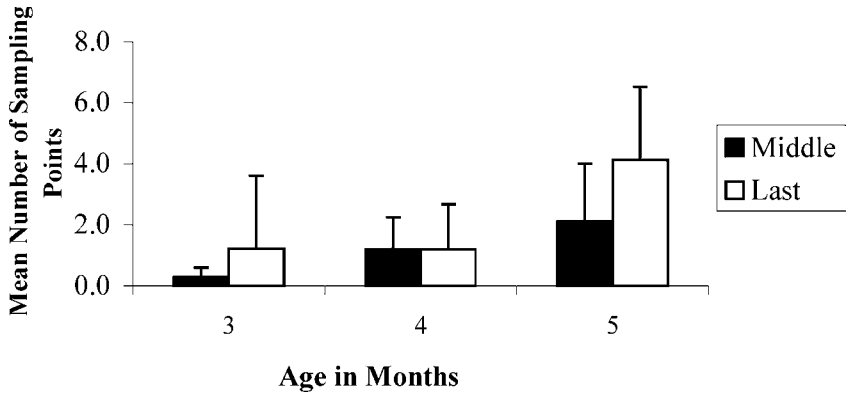


Fig. 5. Changes with age in the traveling position of the infant.

Time Budget and Patterns

Our analyses of infant time budgets reflect their activities during the period when adult owl monkeys were most active. During the 1st 2 mo the infant's allocation of time to the various activities is significantly different from the time budget of the other members of the group (Figs. 7a,b). Then, the infant would normally rest while the nearest individual fed, moved or

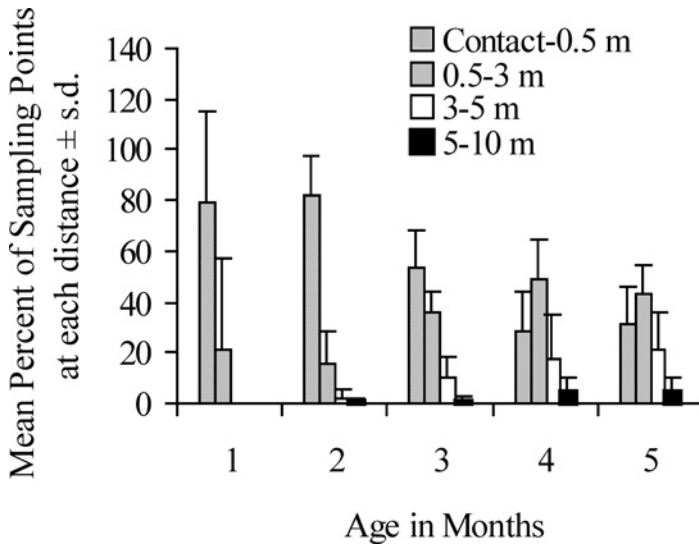


Fig. 6. Changes with age in the distance to nearest subject.

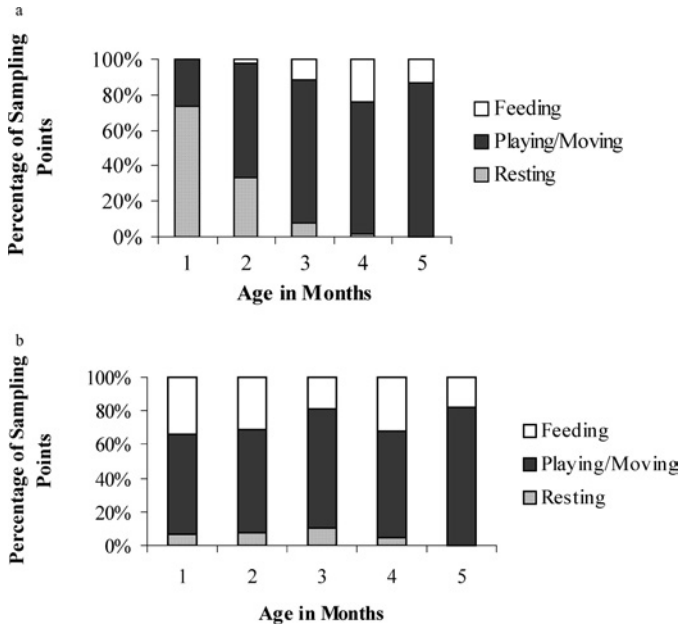


Fig. 7. Time budgets of infant (a) and nearest individual (b).

played. During the 3rd mo the time budgets became very similar. The infant tended to be somewhat more active than the adults from then on probably due to its increase in locomotor activity and play with siblings.

Suckling Behavior

We observed 33 episodes of nursing ($n = 7$ infants). The observed nursing episodes were quite evenly distributed among the various ages. We recorded a minimum of 4 and a maximum of 9 episodes for each mo. One of the infants provided *ca.* 50% of the observations ($n = 15$ episodes), whereas we observed the remainder nursing only once ($n = 1$ infant), 2 ($n = 2$ infants), 3 ($n = 2$) or 6 times ($n = 1$ infant). The mean duration of the nursing episodes is 69 sec (s.d. 25, range: 31–160, $n = 25$ episodes).

Once the infant moved independently, nursing only occurred following an approach by the infant to its mother ($n = 10$). We never observed nursing after an approach of the mother to the infant. After nursing, the infant was more likely to return to the nonnursing adult, than to remain with the mother. On 15 occasions the infant returned to the nonnursing adult after

Table III. Manipulation of twigs or food by infant owl monkeys, aged 1–4 mo, while riding on the parents or independent

Age (mos)	ON parents	OFF parents	N
1	6	2	2
2	33	29	3
3	4	15	4
4	0	9	3

N = number of infants.

nursing, whereas it only twice remained with the mother. Although we observed the mother rejecting the infant for the first time in the 11th wk, the infants were still nursing at 5 mo. Moreover, we observed infants in nipple contact when they were 8 mo old, which suggests that they might have still been nursing.

Feeding on Solid Food

Infants began to explore, to manipulate and to consume solid foods during the 2nd mo (Table III), while riding dorsally on a parent or while moving about independently. By the 3rd mo most food manipulation and consumption occurred while infants were independent. We observed them eating solid foods during 40 observation sessions ($n = 5$ infants).

They consumed solid foods during 44% of the observation sessions during the 2nd mo, 65% in the 3rd mo, 82% in the 4th mo and 86% during the 5th mo. They ate fruits in 82% of sessions and leaves in 28% of them. The fruit sources comprised *Sideroxylon obtusifolium*, *Ficus sp.*, *Myrcianthes pungens*, *Phytolacca dioica*, *Sapium sp.*, *Sebastiania sp.*, *Inga verna*, one unidentified epiphyte and 2 unidentified vines. Infants also ate new leaves from *Gleditsia amorphoides*, *Myrcyanthes pungens* and *Inga uruguensis*.

Food sharing was relatively infrequent. We only observed it on 5 occasions ($n = 4$ infants), twice with the adult male, twice with the carrier and once with a 2-year-old juvenile.

SOCIAL INTERACTIONS

Grooming

Social grooming is relatively infrequent in owl monkeys (Dixon and Fleming, 1981; Moynihan, 1964). We recorded 51 occasions of social

grooming ($n = 6$ infants). Most social grooming was directed by parents to the infant (38/51). There is no significant difference in the amount of social grooming directed to the infant by the mother (12/21) and father (9/21) in the only group wherein we could identify the male unequivocally. Juveniles also groomed the infant, though less often than the adults did (8/51). The infants rarely groomed the parents (2/51) and their siblings (3/51).

Play

We observed play during *ca.* 25% of the observation sessions (20 sessions, $n = 4$ infants). All of them occurred when the infant was >2 mo old. Before then, we saw no play. During the 1st 2 mo most play consisted of the infant moving and jumping around other members of the group or playing with twigs and leaves while they were regrouping, huddling and preparing to sleep. When the infants were 3-mo old, they started chasing juveniles in the group. The chasing always occurred in circles within the crown of a tree, in dense foliage consisting of vines and tangles. During play bouts, the monkeys stopped, grabbed each other, and then resumed chasing. When the infant was older (*ca.* 5 mo), play chases continued, but distances got longer and the individuals could jump and run between 2 or 3 trees. The chases sometimes included both 1-yr-old and 2-yr-old juveniles. We observed adults taking part in chases on only 3 occasions.

DISCUSSION

Despite the marked differences between free-ranging and captive environments, there are some obvious similarities between *Aotus azarai* in Argentina, and captive family groups of *A. lemurinus*, *A. azarai boliviensis* and *A. trivirgatus* as regards their behavior and temporal patterning of developmental events (Dixson and Fleming, 1981; Jantschke *et al.*, 1996; Wright, 1984).

In the wild, as in captivity, newborn owl monkeys cling ventrolaterally, in the flexure of the mother's thigh. Ventrolateral, or ventral (abdominal) carrying positions occur most frequently during the 1st 2 postnatal weeks in free-ranging *Aotus azarai*, but thereafter the infant is increasingly on the dorsal surface of the parent. In captivity, owl monkey infants may cling to the females' back for brief periods, even during the 1st postnatal week; however, we did not observe this in free-ranging owl monkeys. Observations in captivity have established that the mother carries the single offspring during the 1st wk in *Aotus lemurinus* (Dixson and Fleming,

1981) and during the 1st wk in *A. azarai boliviensis* (Jantschke *et al.*, 1996), but thereafter it is the adult male that takes over the role. Usually we could not identify the sex of the parent carrying an infant. However, it was clear that infants transferred actively between their parents, as in captivity. In free-ranging groups of *Aotus azarai* most transfers occurred when infants were 4–7 wk old, which is correlated with periods of increased locomotor activity, whilst infants were riding dorsally on their parents. In captivity, infant *Aotus lemurinus* transferred between parents between 2 and 9 wk and many transfers from the mother to the father occurred after the infant had suckled and was then rejected by the mother.

Suckling bouts are characteristically brief in owl monkeys, ranging between 31–160 sec (mean = 69 sec) in free-ranging *Aotus azarai* and 7–160 sec (mean = 27 sec) in captive *A. lemurinus*. Unlike many Old World monkeys, infant owl monkeys do not remain on the mother's nipple for extended periods. Rather than providing comfort and extended periods of physical contact with their offspring, it appears that female owl monkeys have evolved mechanisms to reject the developing offspring once suckling is complete and to encourage it to transfer to the adult male (Dixson and Fleming, 1981). Accordingly, one could hypothesize that, like titi monkeys (Hoffman *et al.*, 1995; Mendoza and Mason, 1986a) owl monkey infants may be primarily attached to the father.

Infant owl monkeys begin to get off their parents during the 4th wk in captivity, which we rarely observed before the 4th or 5th wk in free-ranging groups. In captivity, infants are off their parents during 50–75% of their active periods when they are between 7 and 11 wk old. They move independently of both parents during >90% of the time when they are 15–18 wk old, which agrees with observations on free-ranging *Aotus azarai*, because infants traveled separately of their parents 40% of the time when they were 3 mo old, and by the 5th mo they were able to travel independently between trees, without the aid of other group members. Infants *Aotus nigriceps* in Perú also traveled independently by 5 mo (Wright, 1984)

In captivity, infant *Aotus lemurinus* begin to consume solid food at 35–60 d, and by 4–5 mo they are weaned. Parallel observations in Argentina indicate that infant *Aotus azarai* begin to manipulate twigs and food items during the 2nd mo, and that by 4 mo they eat fruits and, to a lesser extent, leaves of a variety of plants. However, suckling bouts still occur, and 8-mo-old juveniles still occasionally attempt to take the nipple. Food sharing between weaned infants and other group members occurs rarely under natural conditions. Conversely, food sharing was prevalent among owl monkeys in captivity (Feged *et al.*, 2002; Wright, 1984).

Among monogamous New World monkey species, older siblings and parents may carry young infants in the group (*Callithrix jacchus*: Rothe *et al.*, 1993; *Saguinus fuscicollis*: Vogt *et al.*, 1978). We did not observe it, and it has been recorded infrequently in captive groups of owl monkeys (Dixson and Fleming, 1981; Jantschke *et al.* 1996). Juvenile *Aotus azarai* played with and groomed younger siblings on several occasions. However, most grooming bouts involved parents grooming infants. In captive *Aotus lemurinus*, adults of both sexes groom the offspring with equal frequency and anogenital stimulation often stimulates the infant to urinate or defecate.

The Gran Chaco of Argentina represents a relatively harsh environment for *Aotus azarai*. There are marked seasonal changes in temperature, precipitation, and food availability in the semideciduous gallery forests of Formosa, where owl monkeys are seasonal breeders (Fernandez-Duque *et al.*, 2002). They have adopted a cathemeral activity pattern, which allows groups to remain active during the daylight hours, as well as at night (Fernandez-Duque, 2003; Fernandez-Duque and Erkert, 2004). Despite the constraints upon behavior and reproduction, the development of infant *Aotus azarai* that we observed is very similar, qualitatively and temporally to that described of captive breeding groups of Colombian (*Aotus lemurinus*) and Bolivian owl monkeys (*A. azarai boliviensis*) living in controlled temperature, illumination and food availability (Dixson, 1983; Dixson, 1994; Dixson and Fleming, 1981; Jantschke *et al.*, 1996).

Hershkovitz (1983) postulated that there are 9 species of owl monkeys, whereas Ford (1994) recognized 5–7 species. Both authorities agree that the genus is divisible into 2 species groupings: the grey-necked group north of the Amazon River and the red-necked group south of the river. *Aotus lemurinus* belongs to the grey-necked group, whereas *A. azarai* belongs to the southern group. The similarities in postnatal development, studied under markedly differing conditions, indicates that their behavioral patterns probably represent robust features of infant development for *Aotus*.

ACKNOWLEDGMENTS

We are most grateful to the Zoological Society of San Diego for supporting the research. We thank each of the volunteers and students who made this research possible by spending long hours in the forest: M. Chomnalez, M. Giménez, R. Navarro, P. Ramirez-Llorens and L. Tula. Special thanks to the managers of Estancia Guaycolec, E. Arauz and J. Adams for their continuous support. We thank Claudia R. Valeggia and 2 anonymous reviewers for their useful comments on the manuscript.

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