

## Adult male replacement and subsequent infant care by male and siblings in socially monogamous owl monkeys (*Aotus azarai*)

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**Abstract** Owl monkeys (*Aotus azarai*) are small, territorial, socially monogamous primates that show intense infant care by the adult male in the group. It has been hypothesized that male care may be adaptive because it increases offspring survival and/or reduces the metabolic costs to the female of raising the offspring. Alternatively, males may provide care even when they are not related to the infants to increase future reproductive opportunities. We describe changes in infant care patterns that took place after the eviction of the resident male by a solitary male in an owl monkey population in the Argentinean Chaco. The resident male and mother provided all infant care during the first month of life of the infant, until the male was evicted. During the three-day male replacement event, care of the infant was shared among the mother, a four-year-old sister, and a one-year-old brother. The new male began contributing to infant care soon after entering

the group, carrying, and interacting socially with the infant in much the same way as any male regularly does. However, despite receiving biparental care from both the original and new resident males, the infant disappeared at the age of four months and was presumed dead. These are the first reports of care by sibling and by non-putative fathers in wild owl monkeys. Given the significant amount of time that new pairs of owl monkeys spend before reproducing, it is possible that male care in owl monkeys functions as mating effort as much as or more than parenting effort.

**Keywords** Monogamy · Take over · Paternal care · Sibling care

### Introduction

Owl monkeys are socially monogamous primates that show intense male care of offspring. It has been suggested that in monogamous species, given the relatively high costs to a female of raising and caring for offspring, males may care directly for infants or provide some kind of indirect services to females (Tardif 1984; Wright 1984, 1986; Van Schaik and Dunbar 1990; Tardif 1994; Van Schaik and Kappeler 1997; Runcie 2000; Sommer 2000). The male-care hypothesis predicts that males should provide infant care when paternity certainty is high or in exchange for future reproductive opportunities even when paternity certainty is low (Smuts and Gubernick 1992). It is, moreover, predicted that in the absence of male care the development and survival of infants may be affected. We describe here changes in the patterns of infant care after the replacement of the putative father in one focal social group by a solitary male.

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## Methods

The owl monkey population of Riacho Pilagá in Argentina (58°11'W, 25°58'S) consists of socially monogamous groups and solitary individuals going through natal or secondary dispersal (Fernandez-Duque et al. 2006; Fernandez-Duque 2007). The focal social group included an adult resident male and an adult resident female who had been paired for at least two years, a four-year-old female, a two-year-old female, a one-year-old male, and an unsexed infant. The focal solitary male had been ranging alone since 15th June 2002 when he was captured and radio-collared.

We collected systematic data during twenty minutes of focal observations of all members of the group and the solitary before and after the replacement event (Di Fiore et al. 2006, 2007). During following of the group we recorded whether the infant was independent or not, the position of the infant on the individual transporting it (dorsal, ventral, or ventrolateral, resting in the flexure of the carrier's thigh), and the activity of the infant as an instantaneous point sample every two minutes, and we noted all occurrences of a set of additional social behavior of interest that occurred between sampling points. We collected additional data ad libitum during the three-day replacement event. Data recorded with instantaneous sampling are presented as percentage of number of sampling points, and whenever used, "time" refers to the percentage of sampling points. For the analysis of changes with age, the data collected were averaged across observation sessions for each month of life of the infant.

We collected data during 27 days between 9th October 2003 and 3rd March 2004. We observed the group and solitary male for 66 h and collected 39 h of systematic data distributed in three periods:

1. infant birth to replacement of the resident male ( $n = 10$  days of observation, 15 h contact, 4 h focal);
2. replacement of the resident male (8–12th November, 20 h contact, ad libitum data); and
3. after male replacement and until the infant disappeared ( $n = 14$  days, 17 h contact, 6 h focal).

## Results

### Biparental care by the resident pair

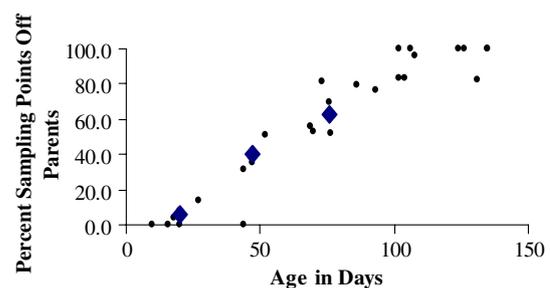
The infant was born between 6 and 9th October 2003. During the first month of life, the infant was almost never "off" the mother (Fig. 1), riding dorsally (49%), ventrally (20%), or ventrolaterally (30%) on her. During this period,

siblings never carried the infant and the resident male did so only 6% of the time. When the mother was transporting the infant, she was first, second, or in the middle of the group most of the time (84%), but seldom in the last position (5%) or one before last (11%). When the resident male carried the infant, he was typically last in the group progression, and he took long rests, sometimes even with his eyes closed. On 3rd November, when the resident female and resident male participated in agonistic interactions with an individual outside the group, the infant was on the female. On 4th November, we captured the resident male to fit him an actometer collar (Fernandez-Duque and Erkert 2006). He was apparently in good health, but his weight (1,120 g) was lower than when he had been captured on 13th March 2002 (1,450 g).

### Male replacement period

On 8th November, the solitary male was observed within the group's territory after having ranged during the previous months over the territories of other groups in the vicinity, but he did not interact with the focal group. Two days later, the resident male was found limping and separated from the group and the solitary male was seen close to the group for the first time. The resident female approached the solitary male once, but then returned to the resident male. The resident male went to sleep together with the group at 0736 hours, while we could hear the solitary male giving loud contact vocalizations ("hoots") ~15 m away. In the afternoon, the resident male was still limping, but continued to range with other members of the group. At 1940 hours, the solitary male was still in the area as indicated by hoots and his radiocollar signal.

On 11th November, two observers tracked the group and solitary male simultaneously all day. The resident male was still ranging with the group, but usually lagging ~30 m behind. At 0655 hours, we captured the resident male to remove his actometer collar and released him at 0930 hours.



**Fig. 1** Time spent off parents by the focal infant (*large rhomboid symbols*) and infants observed in groups where no male replacement had taken place (*small round symbols*). The figure has been modified from Rotundo et al. (2005) to incorporate the new data presented here

There was no indication that the collar had caused him any problems, but he had bites on both legs, one of his ankles was very swollen, and he had blood stains over his legs. He weighed 110 g less than the week before. During the rest of the day, all group members approached the resident male at least once, but he spent most of his time alone ~15–30 m away from the group. The solitary male tried to approach the resident female a few times, but she retreated. The resident male moved towards the solitary male, and the latter retreated. The spatial arrangement during that day could be summarized as follows:

1. the solitary male wandering near the group, sometimes approaching all members, sometimes being chased away by all members;
2. the resident male ranging apart, but sometimes approached by other group members; and
3. the rest of the group splitting their time between the two males.

We did not observe any overt aggression or physical contact between the resident and solitary male but we recorded lots of hoot vocalizations by the solitary male and repeated scent marking by both males.

On 12th November, we observed the group between 0606 and 0924 hours. The resident female and solitary male were observed sitting together in contact and approaching each other. The solitary male had the fourth digit of the right foot hanging as if it were broken. The female tended to move ahead of the group, and once we observed the solitary male chasing and grabbing her. The solitary male interacted with all members of the group except the infant. During this time, the resident male was ~80 m from the group, sitting quietly, foraging and resting. He was never seen interacting with the group again, and he ranged alone until he was found dead 2 months later on 8th January.

#### Alloparental care by the replacement male and siblings

Alloparental behavior first took place on 10th and 11th November during the process of replacement, when the infant's four-year-old sister waited for the infant and assisted it to climb on her back. She moved last in the group over a 12 min period until eventually the mother approached her and the infant descended from its sister and climbed on its mother. The one-year-old brother also carried the infant over a period of 10 min while traveling in last position, after which the infant changed to the mother. The rest of the time, the infant was always carried by the mother and never by the solitary male who became the new resident.

The infant was independent 40% of the time during its second month of life and 63% of the time during the third

month (Fig. 1). Over this period, the mother, older sister, and new resident male transported the infant for similar periods of time (31, 37 and 31%, respectively). When the infant was three months old, the new resident male transported the infant the most (67%), followed by the older sister (29%) and the mother (4%). The individual carrying the infant tended to be last in group progressions more frequently (62%) than first (13%) or in the middle (25%).

Regarding the nature of social interactions, all non-mother members of the group interacted with the infant. Following distress vocalizations by the infant, we observed the older sister, the younger brother, and the new resident male all approaching the infant and offering their backs. Following retrieval, it happened once that the older sister tried to pull the infant off of her back while it was screaming. When the sister succeeded and moved away, the solitary male approached and retrieved it. During this period we observed the infant playing with the new resident male, but we never observed the mother approaching and retrieving the infant. Quite the contrary, we observed the mother grabbing and trying to remove the infant from her back twice.

Grooming is relatively infrequent in wild owl monkeys. In the presence of a resident male, siblings rarely groomed an infant (Rotundo et al. 2005), but after replacement, the older sister was the groomer in three of the five cases where we observed the infant being groomed. On 26th January the infant was observed for the last time. It was in apparent good health while being transported by the solitary male.

## Discussion

Our observations of infant care by the original resident male during the first month of life of the infant are in general agreement with previous reports of infant care in this species (Rotundo et al. 2005), and in other species of owl monkey (Dixson and Fleming 1981). The mother was the main carrier during the first few weeks of life. However, it is worth noting that we first saw the resident male carrying the infant when the infant was a month old, and we also observed him rejecting the infant, which is somewhat unusual in that resident males normally begin helping earlier. It was also unusual to see the resident male moving last while transporting the infant. Adults carrying infants only rarely travel in last position during group movements (Rotundo et al. 2005). It is thus possible that deteriorating health of the resident male may have been responsible for these somewhat anomalous patterns. Given our experience conducting over 150 captures and releases of owl monkeys since 2000 (Fernandez-Duque and Rotundo 2003), we think it is unlikely that our capturing of the resident male could have led to this unusual

behavior. We noted no differences in the development of the infant during the second month of life, after integration of the new resident male into the group. In other words, within a few weeks of the replacement of the original resident male, there were no obvious differences between the patterns of care provided to this infant and those provided to infants by resident males and females in other groups (Fig. 1).

Despite its seemingly normal development, the infant did not survive. Although it is of course possible that our sampling regime was not sensitive enough to detect subtle variations in the pattern of male care that may have influenced the likelihood of infant survival, we believe it unlikely. In captivity, a fatherless owl monkey infant also survived after being cared by his sister, but the lack of paternal care in that group led the infant to become independent much earlier than infants receiving care from fathers (Jantschke et al. 1996). Although this earlier locomotor independence did not affect infant survival in the safe environment of captivity, it may prove fatal in the wild.

These are the first observations of sibling care reported for wild owl monkeys and the first time care by a non-putative father is described. Why did the solitary male care for the infant? In the absence of genetic data, and to the extent that this is a singular observation, we can only suggest a possible explanation worth exploring in the future. Newly formed pairs of owl monkeys almost always take at least a year to reproduce (Fernandez-Duque 2007), suggesting there is a period of evaluation of the pairmate as a potential parent. For an incoming male, providing infant care may be a strategy for developing or securing a bond with the resident female in anticipation of future reproductive opportunities. In other words, male care could function as mating effort as much as or more than parenting effort (Smuts and Gubernick 1992).

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