

1 Adult Male Replacement and Subsequent Infant Care by Male and Siblings in Socially  
2 Monogamous Owl Monkeys (*Aotus azarai*).

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12 Short title: Male replacement and paternal care in owl monkeys

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## 24 ABSTRACT

25 Owl monkeys (*Aotus azarai*) are small, territorial, socially monogamous primates  
26 that show intense infant care by the adult male in the group. It has been hypothesized  
27 that male care may be adaptive because it increases offspring survival and/or reduces  
28 the metabolic costs to the female of raising the offspring. Alternatively, males may  
29 provide care even when they are not related to the infants to increase future  
30 reproductive opportunities. We describe changes in infant care patterns that took place  
31 following the eviction of the resident male by a solitary male in an owl monkey  
32 population in the Argentinean Chaco. The resident male and mother provided all infant  
33 care during the first month of life of the infant, until the male was evicted. During the  
34 3-day male replacement event, care of the infant was shared among the mother, a 4-  
35 year-old sister, and a 1-year-old brother. The new male began contributing to infant  
36 care soon after entering the group, carrying, and interacting socially with the infant in  
37 much the same way as any male regularly does. However, despite receiving biparental  
38 care from both the original and new resident males, the infant disappeared at the age of  
39 four months and was presumed dead. These are the first reports of care by sibling and  
40 by non-putative fathers in wild owl monkeys. Given the significant amount time that  
41 new pairs of owl monkeys spend before reproducing, it is possible that male care in owl  
42 monkeys functions as mating effort as much as or more than parenting effort.

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44 Key words: monogamy, take over, paternal care, sibling care

45

## 46 INTRODUCTION

47 Owl monkeys are socially monogamous primates that show intense male care of  
48 offspring. It has been suggested that in monogamous species, given the relatively high  
49 costs to a female of raising and caring for offspring, males may care directly for infants  
50 or provide some kind of indirect services to females (Tardif 1984; Wright 1984; Wright  
51 1986; Van Schaik and Dunbar 1990; Tardif 1994; Van Schaik and Kappeler 1997;  
52 Runcie 2000; Sommer 2000). The male care hypothesis predicts that males should  
53 provide infant care when paternity certainty is high or in exchange for future  
54 reproductive opportunities even when paternity certainty is low (Smuts and Gubernick  
55 1992). Moreover, it is predicted that in the absence of male care the development and  
56 survival of infants may be affected. We describe here changes in the patterns of infant  
57 care following the replacement of the putative father in one focal social group by a  
58 solitary male.

59

## 60 METHODS

61 The owl monkey population of Riacho Pilagá in Argentina (58°11' W, 25°58' S)  
62 consists of socially monogamous groups and solitary individuals going through natal or  
63 secondary dispersal (Fernandez-Duque et al. 2006; Fernandez-Duque 2007). The focal  
64 social group included an adult resident male and an adult resident female who had been  
65 paired for at least two years, a four-year-old female, a two-year-old female, a 1-year-old  
66 male, and an unsexed infant. The focal solitary male had been ranging alone since June  
67 15th 2002 when he was captured and radio-collared.

68 We collected systematic data during 20-min focal observations of all members of  
69 the group and the solitary before and after the replacement event (Di Fiore et al. 2006;

70 Di Fiore et al. 2007). During follows, we recorded whether the infant was independent  
71 or not, the position of the infant on the individual transporting it (dorsal, ventral, or  
72 ventrolateral, resting in the flexure of the carrier's thigh), and the activity of the infant  
73 as an instantaneous point sample every two minutes, and we noted all occurrences of a  
74 set of additional social behaviors of interest that occurred between sampling points. We  
75 collected additional data *ad libitum* during the three-day replacement event. Data  
76 recorded with instantaneous sampling are presented as percentage of number of  
77 sampling points, and whenever used, "time" refers to the percentage of sampling points.  
78 For the analysis of changes with age, the data collected were averaged across  
79 observation sessions for each month of life of the infant.

80 We collected data during 27 days between October 9<sup>th</sup>, 2003 and March 3<sup>rd</sup>, 2004.  
81 We observed the group and solitary male during 66 hours and collected 39 hours of  
82 systematic data distributed in three periods: 1- infant birth to replacement of the resident  
83 male (n = 10 days of observation, 15 hrs contact, 4 hrs focal), 2- replacement of the  
84 resident male (Nov 8-12<sup>th</sup>, 20 hrs contact, *ad libitum* data), and 3- after male  
85 replacement and until the infant disappeared (n = 14 days, 17 hrs contact, 6 hrs focal).

86

## 87 RESULTS

### 88 **Biparental Care by the Resident Pair**

89 The infant was born between October 6<sup>th</sup> and 9<sup>th</sup>, 2003. During the first month of  
90 life, the infant was almost never "off" the mother (Figure 1), riding dorsally (49%),  
91 ventrally (20%), or ventrolaterally (30%) on her. During this period, siblings never  
92 carried the infant and the resident male did so only 6% of the time. When the mother  
93 was transporting the infant, she was first, second, or in the middle of the group most of

94 the time (84%), but seldom in the last position (5%) or one before last (11%). When the  
95 resident male carried the infant, he was typically last in the group progression, and he  
96 took long rests, sometimes even with his eyes closed. On November 3<sup>rd</sup>, when the  
97 resident female and resident male participated in agonistic interactions with an  
98 individual outside the group, the infant was on the female. On November 4<sup>th</sup>, we  
99 captured the resident male to fit him an actometer collar (Fernandez-Duque and Erkert  
100 2006). He was apparently in good health, but his weight (1120 grs) was lower than  
101 when he had been captured on March 13<sup>th</sup>, 2002 (1450 grs).

102

### 103 **Male Replacement Period**

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

114 On November 11<sup>th</sup>, two observers tracked the group and solitary male  
115 simultaneously all day. The resident male was still ranging with the group, but usually  
116 lagging ~ 30 m behind. At 0655h, we captured the resident male to remove his  
117 actometer collar and released him at 0930h. There was no indication that the collar had

118 caused him any problems, but he had bites on both legs, one of his ankles was very  
119 swollen, and he had blood stains over his legs. He weighted 110 grams less than the  
120 week before. During the rest of the day, all group members approached the resident  
121 male at least once, but he spent most of his time alone ~15 to 30 m away from the  
122 group. The solitary male tried to approach the resident female a few times, but she  
123 retreated. **The resident male moved towards the solitary male,** and the latter retreated.  
124 The spatial arrangement during that day could be summarized as follows: 1- the solitary  
125 male wandering near the group, sometimes approaching all members, sometimes being  
126 chased away by all members, 2- the resident male ranging apart, but sometimes  
127 approached by other group members, and 3- the rest of the group splitting their time  
128 between the two males. We did not observe any overt aggression or physical contact  
129 between the resident and solitary male, but we recorded lots of hoot vocalizations by the  
130 solitary male and repeated scent marking by both males.

131 On November 12<sup>th</sup>, we observed the group between 0606h and 0924h. The resident  
132 female and solitary male were observed sitting together in contact and approaching each  
133 other. The solitary male had the fourth digit of the right foot hanging as if it were  
134 broken. The female tended to move ahead of the group, and once we observed the  
135 solitary male chasing and grabbing her. The solitary male interacted with all members  
136 of the group except the infant. During this time, the resident male was ~80 m from the  
137 group, sitting quietly, foraging and resting. He was never seen interacting with the  
138 group again, and he ranged alone until he was found dead two months later on January  
139 8<sup>th</sup>.

140

## 141 **Alloparental Care by the Replacement Male and Siblings**

142 Alloparental behavior first took place on November 10<sup>th</sup> and 11<sup>th</sup> during the process  
143 of replacement, when the infant's 4-year old sister waited for the infant and assisted it to  
144 climb on her back. She moved last in the group over a 12 min period until eventually  
145 the mother approached her and the infant descended from its sister and climbed on its  
146 mother. The 1-year old brother also carried the infant over a period of 10 min while  
147 travelling in last position, after which the infant changed to the mother. The rest of the  
148 time, the infant was always carried by the mother and never by the solitary male who  
149 became the new resident.

150 The infant was independent 40% of the time during its second month of life and  
151 63% of the time during the third month (Figure 1). Over this period, the mother, older  
152 sister and new resident male transported the infant for similar periods of time (31%,  
153 37% and 31% respectively). When the infant was three-month-old, the new resident  
154 male transported the infant the most (67%), followed by the older sister (29%) and the  
155 mother (4%). The individual carrying the infant tended to be last in group progressions  
156 more frequently (62%) than first (13%) or in the middle (25%).

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

164 mother approaching and retrieving the infant. Quite the contrary, we observed the  
165 mother grabbing and trying to remove the infant from her back twice.

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

171

## 172 DISCUSSION

173 Our observations of infant care by the original resident male during the first month  
174 of life of the infant are in general agreement with previous reports of infant care in this  
175 species (Rotundo et al. 2005), as well as in other species of owl monkeys (Dixon and  
176 Fleming 1981). The mother was the main carrier during the first few weeks of life.  
177 However, it is worth noting that we first saw the resident male carrying the infant when  
178 the infant was a month old, and we also observed him rejecting the infant, which is  
179 somewhat unusual in that resident males normally begin helping earlier. It was also  
180 unusual to see the resident male moving last while transporting the infant. Adults  
181 carrying infants only rarely travel in last position during group movements (Rotundo et  
182 al. 2005). It is thus possible that deteriorating health of the resident male may have  
183 been responsible for these somewhat anomalous patterns. Given our experience  
184 conducting over 150 captures and releases of owl monkeys since 2000 (Fernandez-  
185 Duque and Rotundo 2003), we think it is unlikely that our capturing of the resident male  
186 could have led to this unusual behavior. We noted no differences in the development of  
187 the infant during the second month of life, following the integration of the new resident

188 male into the group. In other words, within a few weeks of the replacement of the  
189 original resident male, there were no obvious differences between the patterns of care  
190 provided to this infant and those provided to infants by resident males and females in  
191 other groups (Figure 1).

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

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

211

## 212 ACKNOWLEDGEMENTS

213 The authors are grateful to the Wenner-Gren Foundation, the L.S.B. Leakey  
214 Foundation, the J. William Fulbright Scholar Program, Primate Conservation, Inc., Idea  
215 Wild, New York University, and the Zoological Society of San Diego for their support.  
216 Special thanks are also due to the Argentinean and Formosa Province government for  
217 their continued interest in our primate research, and to Federico Middleton and Conrado  
218 Cimino of Bellamar Estancias for logistical support at Estancia Guaycolec. EFD  
219 conducted this research while a postdoctoral fellow of the Zoological Society of San  
220 Diego and an Adjunct Researcher of the CECOAL-Conicet (Argentina). The research  
221 described here was done in full agreement with all Argentinean legislation and was  
222 approved by the IACUC committee of the Zoological Society of San Diego.

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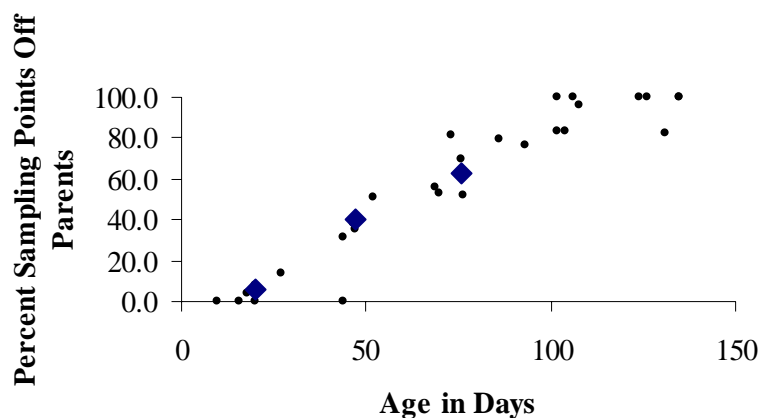
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- 272 Figure 1. Time spent off parents by the focal infant (large rhomboid symbols) and infants  
 273 observed in groups where no male replacement had taken place (small rounded symbols).

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