

SHORT COMMUNICATION

Adoption of a Wild Orphaned Ringtailed Lemur Infant by Natal Group Members: Adaptive Explanations

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ABSTRACT. In December 1992 an infant ringtailed lemur, approximately 7 weeks of age, was orphaned in one of the regularly-censused social groups at the Beza-Mahafaly Reserve, southwestern Madagascar. The infant was initially adopted by a subadult (2 yr-old) male from the group. Continuous-time focal animal data were collected for a 12-hr period, from the time that the infant was retrieved by the young male, in order to document the adoption process. Ten members of the infant's social group (total group number = 18) engaged in infant care behaviors over the 12-hr period. The subadult male spent the most time engaged in infant care, and he and one adult female exhibited the highest frequency of caregiving behaviors over the 12-hr period ($p < 0.001$). Four adult males also initially cared for the infant. The orphan was one of only six infants in the reserve population to survive that year. She was censused two years later as an adolescent member of her natal group. Adaptive explanations for this adoption vary depending upon the caregiver. For the subadult male and adult female caregivers, kin selection can be suggested, as the infant was related to all females and immature animals in the group. Adult males may have exhibited caregiving behaviors as a strategy related to affiliation with adult females which could lead to potential mating and reproductive success.

Key Words: Adoption; Ringtailed lemur; Orphan; Adaptive explanations.

INTRODUCTION

Adoption of orphaned nonhuman primates has been documented in numerous anthropoid species (see THIERRY & ANDERSON, 1986; HRDY, 1976). THIERRY and ANDERSON (1986) suggest that orphaning is not a rare event in naturally-occurring primate populations, due to factors such as predation, disease, and injury, all of which affect lactating adult females. In this paper, I will describe the adoption, by group members of differing age and sex classes, of a 7 week-old, orphaned female ringtailed lemur at the Beza-Mahafaly Reserve in southwestern Madagascar, and discuss the possible adaptive reasons for such an occurrence. This is the first published report of an adoption by prosimian primates in a naturally-occurring situation, although JOLLY observed the adoption of an abandoned ringtailed lemur infant previously (JOLLY, unpubl.).

RIEDMAN (1982) suggests that adoption is an example of apparent altruism, and that such behavior appears inconsistent with classic evolutionary theory. However, since many primate orphans are adopted by female or immature relatives, such caregiving behavior can be explained by kin-selection theory (HAMILTON, 1964), though it is important to consider these on a case-by-case basis. More difficult to explain are adoptions by adult males, who may or may not be related to the orphan, in multimale primate social groups. RIEDMAN (1982) proposes that adoption by adult males may reflect potential reproductive benefits gained through continued

association with infants. THIERRY and ANDERSON (1986) suggest that the costs and benefits of adoption are related to the age and sex of the participants, social and kin relationships, and ecological conditions. Adoption might be expected between close relatives, because overall inclusive fitness can be increased if the infant survives.

STUDY SPECIES, STUDY SITE, AND METHODS

The ringtailed lemur (*Lemur catta*) is characterized by multimale groups, female philopatry, male dispersal, and female dominance (JOLLY, 1966; SUSSMAN, 1977).

The adoption occurred at the Beza-Mahafaly Special Reserve, in southwestern Madagascar. Beza-Mahafaly is the site of a long-term demographic project on individually identified (colored and tagged) ringtailed lemurs begun in 1987 by ROBERT SUSSMAN (1991). Demographic, behavioral, and ecological data were collected on animals residing in the nine groups within the reserve boundaries between 1987 and 1996 (SUSSMAN, 1991; GOULD et al., 1999). Brown group, the group in which the adoption occurred, consisted of four adult females, eight adult males, two adolescent (2 yr-old) males, two adolescent females, three yearlings, and four infants.

The orphaning and subsequent adoption occurred on December 4, 1992. The birth and lactation season of 1992 – 1993 was a period of very high infant- and lactating-female mortality in the ringtailed lemur population at the Beza-Mahafaly Reserve, following a severe two-year drought in the region. Adult female mortality in the reserve population that particular year was 21%, and infant mortality was 80% (GOULD et al., 1999).

Brown group was not one of the groups being studied at the time, but considering that adoption is rarely observed in the wild, the group was followed for the entire day that the adoption occurred. Continuous-time focal animal data (ALTMANN, 1974) were collected for 12 consecutive hours (approximately 06:00 to 18:00), by myself and a research assistant. Frequency and duration of all behaviors exhibited by the infant and all caregivers over the 12-hr period were recorded. We noted which animals exhibited caregiving behaviors, and the type of care given to the infant throughout the day. Subsequent to the day of the adoption, ad lib notes were collected on the infant when the group passed through the researcher's camp. I was able to gather ad lib information on 24 occasions between December 5, 1992 and March 21, 1993. I noted whether or not the infant was nursing when observed, if she was being carried, and if so, by which group member.

OBSERVATION

On the morning of December 4, 1992, a lactating female was found dead on the ground, under a tree, in the researchers' camp. She was identified by her collar and tag as a female from Brown group. This particular group's home range included the research camp, and animals from this group were often seen in and around the camp area. Upon examination, the dead female did not exhibit any observable external injuries, and appeared to be another casualty of the severe drought occurring at the time. Sometime in the early morning she and her infant had fallen out of the tree, but the infant had survived the fall.

The dead female and live infant were placed in a tree near the area where Brown group was feeding. The infant began distress calling, and immediately a subadult male (2 yr-old) from Brown group appeared and presented his back to the infant. The infant then jumped onto the subadult male's back.

In the 12-hr period following retrieval of the infant by the subadult male, ten different group members exhibited caregiving behaviors towards the orphan. The caregivers included three lactating females, four adult males, one yearling, a subadult (2 yr-old) male, and a subadult (2 yr-old) female. Caregiving behaviors included dorsal and ventral carrying, grooming the infant, resting and sitting in contact with the infant, and in the case of one adult female, allowing the infant to nurse for brief periods.

FREQUENCY OF CAREGIVING BEHAVIORS

When considering the frequency of infant care behaviors by the ten caregivers over the 12-hr period, a strong significant difference is found $\chi^2 = 122.52, p < 0.001$ (Fig. 1).

One lactating female (female *No. 1*) with a unweaned infant of her own, and the subadult male that initially retrieved the infant, exhibited much higher frequencies of infant care behaviors than did the other eight group members that participated in the care of the orphan over the 12-hr period. Female *No. 1* suckled, groomed, rested in contact, and occasionally carried the infant (Table 1); however carrying was accompanied by much agonistic behavior towards the orphan, such as nipping or pushing the infant off of her back.

The subadult male's most frequent caregiving behavior over the 12-hr period was carrying the orphan. Of the 20 caregiving behaviors exhibited by this animals, 10 were cases of carrying (Table 1).

Caregiving behaviors over the 12-hr observation period by other group members consisted of dorsal and ventral carrying, grooming the infant, resting and sitting in contact with the infant (Table 1).

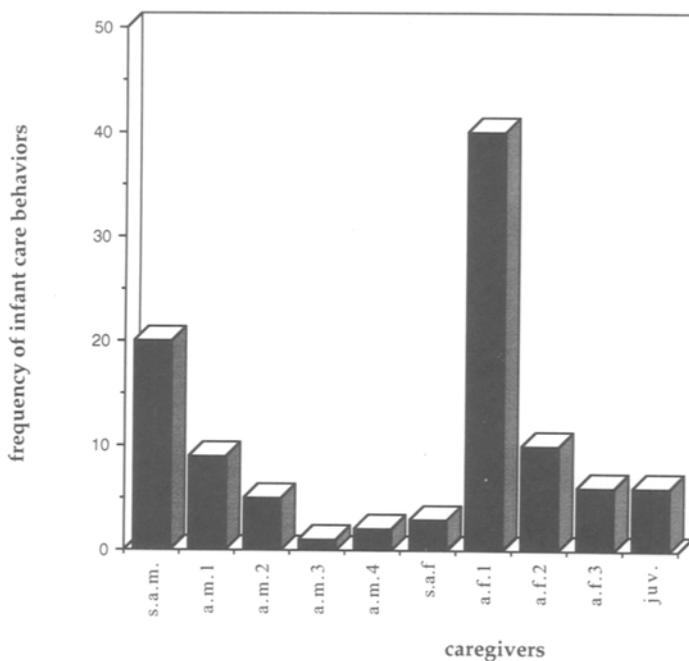


Fig. 1. Frequency of infant care behaviors exhibited by group members over 12-hr period. s.a.m.: Subadult male (2 yr); a.m.: adult male; s.a.f.: subadult female (2 yr); a.f.: adult female; juv.: juvenile (yearling).

Table 1. Breakdown of infant care behaviors by caregiver.

	Sit/rest in contact	Groom infant	Nurse infant	Carry infant
Adult female <i>No. 1</i>	26	4	5	5
Subadult male (2 yr)	5	5	–	10
Adult female <i>No. 2</i> and <i>No. 3</i>	3	10	–	3
Four adult males	12	–	–	9
Subadult female (2 yr)	2	–	–	2
Juvenile (yearling)	4	2	–	–

TIME SPENT IN CAREGIVING BEHAVIOR

Again, the subadult male and adult female *No. 1* spent far more time in the 12-hr period caring for the infant than did other group members [2.5 and 2.2 hr respectively, compared with a mean of 13.5 min for all other individuals: range 3 min (juvenile) to 50 min (adult male)].

Nine days after the adoption episode, adult female *No. 1* lost her own infant, likely due to malnutrition and/or disease brought on by the severe drought. After the death of female *No. 1*'s infant, the orphan was occasionally carried by her and allowed to nurse for brief periods of less than 5 min.

SUBSEQUENT TO THE ADOPTION DAY

The infant was sighted on 24 occasions subsequent to the day of the adoption, between December 5, 1992 and March 21, 1993. On 12 occasions she was observed being carried by female *No. 1*, and on 6 occasions she was carried by the subadult male. The orphan was often heard distress calling if left behind during group movement. In these instances, the subadult male would either retrieve and carry her, or call to her and wait for her to join him.

Until I left the reserve in late March 1993, the orphan was cared for primarily by adult female *No. 1* and the subadult male. When I returned to the reserve in September 1994, the orphan was a 2-yr-old subadult.

DISCUSSION

ADAPTIVE EXPLANATIONS FOR THE ADOPTION

Ringtailed lemur infants are considered precocial among primates. However, wild infants at seven weeks are still highly dependent upon their mothers' milk even though they begin eating solid foods at about 6 weeks of age (GOULD, 1990). They are also carried during group movement until around 9 weeks of age (GOULD, 1990). Thus, a 7-week-old orphan could not survive unless it was adopted. This adoption was unusual in that there were two primary foster parents, and on the day that the infant was orphaned, eight other group members exhibited infant care behaviors.

The most obvious and accepted explanation as to why adoption of orphaned primates occurs is kin selection (HAMILTON, 1964). For a lactating adult female, adoption is costly in terms of her energy expenditure, whether she is suckling her own infant or has lost it (THIERRY & ANDERSON, 1986). However, THIERRY and ANDERSON suggest that altruistic adoption might be expected between close relatives, because overall inclusive fitness can be increased if the infant

survives. In this case, the mother and the lactating female (female *No. 1*) that cared for the orphan were from the same matriline, although the exact degree of relatedness is not known. Female *No. 1* was the only one of four lactating females in the group that allowed the infant to nurse, although not for long periods. She also frequently exhibited agonistic behavior towards the orphan when it jumped on her back to be carried or attempted to nurse. The lactation season is extremely costly for ringtailed lemur mothers, because at the onset of the birth season, they are producing milk during the period of greatest food scarcity (JOLLY, 1984; SAUTHER, 1992, 1993), thus carrying and suckling an extra infant or an infant that is not their own incurs a marked cost for the female, particularly during drought periods. Therefore, it could be suggested that by not allowing long nursing bouts, and by not carrying the infant often, female *No. 1* was promoting the survival of a relative, but was not allowing such caregiving behavior to become overtly physiologically stressful.

As mentioned above, blood relationships within the group were not known, however the subadult male would have been related to the orphan, because he still resided in his natal group, and all immatures in their natal groups are related. By caring for this infant, one could suggest that he was promoting his own inclusive fitness.

More difficult to explain is the fact that four different adult males cared for the orphan the morning that the adoption occurred. Ringtailed lemur females mate with numerous males during their receptive period (KOYAMA, 1988; SAUTHER, 1991), therefore only one, if any, of these four males could have been the father. Thus, such care cannot necessarily be attributed to kin selection theory. If paternity is unlikely, then why would these adult males exhibit caregiving behavior towards the orphan? Adult male ringtailed lemurs do exhibit an interest in infants, and occasionally groom, carry, and play with infants and juveniles (GOULD, 1992, 1994, 1997). Furthermore, affiliation with immatures allows an adult male greater access to, and increased opportunities for social relationships with females, which could potentially lead to enhanced mating opportunities and enhancement of rank (GOULD, 1996, 1997). Such a strategy has been reported in Japanese macaques (HASEGAWA & HIRAIWA, 1980; WOLFE, 1981), baboons (SMUTS, 1985; STRUM, 1987), and Nilgiri langurs (POIRIER, 1968).

ORPHAN'S ROLE IN THE ADOPTION

CLARKE and GLANDER (1981) noted adoptions of four infants in wild howler monkeys, and argue that the success of these adoptions was related to the persistence of the infants, including solicitation of carrying by repeated vocalizations, resistance to being rejected from dorsal riding, and if rejected, immediately returning to the dorsal riding position. CLARKE and GLANDER stress that an infant must solicit care to invoke a response from adults. The ringtailed lemur orphan in this study initially emitted loud distress calls before the subadult male approached and carried her on the morning of the adoption. Later that day, and in the subsequent 3-month period of observation, the infant could often be heard vocalizing loudly when left behind during a group progression or when she could not cross particular arboreal pathways. She was approached and carried by four adult males following such behavior on the morning of the adoption. In the following 3-month period, when the infant was observed vocalizing in this context, the subadult male usually approached and carried her. Thus, it seems reasonable to suggest that the orphan's own persistence was a crucial factor in her survival to adulthood.

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