Grandmaternal Infant Carrying in Wild Northern Muriquis (*Brachyteles hypoxanthus*)

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Introduction

Opportunities for grandmothers and other older matrilineal kin to invest in their grandchildren or younger maternal relatives are affected by whether females remain and reproduce in their natal groups. They may also be mediated by the trade-offs between investing in their own offspring versus those of their relatives. Indeed, the evolution of post-reproductive life spans in human females has been attributed to the fitness benefits that older matrilineal kin may gain by investing in their relatives' offspring instead of their own (Hrdy, 1981; Hawkes *et al.*, 1998). Some types of allomaternal investment, such as agonistic support or babysitting, can be provided irrespective of the female's own reproductive condition, while other types, such as infant carrying during travel or feeding, may be more limited if the female is already carrying an infant of her own (Paul, 2005). In Hanuman langurs (*Semnopithecus entellus*), experienced females with weaning infants or no infants accounted for roughly 10% of all allomothering attempts (Hrdy, 1977: 210), and in Japanese macaques (*Macaca fuscata*), the survivorship of infants to 12 months was significantly higher if their post-reproductive grandmothers were present than if their grandmothers were still reproducing or no longer alive (Pavelka *et al.*, 2002). In captive vervet monkeys (*Chlorocebus aethiops*), grandmothers without infants had significantly higher rates of caring for grandchildren than grandmothers with infants (Fairbanks, 1988: 437).

Northern muriquis (*Brachyteles hypoxanthus*) live in patrifocal societies in which allomaternal care of any type is rare (Odalia-Rímoli, 1998; Guimarães and Strier, 2001; Martins *et al.*, 2007). Grandmothers rarely have opportunities to interact with maternal grandchildren because daughters typically disperse from their natal groups prior to the onset of puberty (Printes and Strier, 1999; Strier and Ziegler, 2000). The only previous known muriqui grandmother of two daughters that reproduced in their natal group was caring for her own infants when her grandchildren were born, and was never observed to carry them. In this paper, we present data on infant-carrying by a second grandmother that did not have her own infant at the time.

Methods

The study was conducted at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala (RPPN-FMA) in Caratinga, Minas Gerais, Brazil. The 957-ha forest supports four groups of northern muriquis, and has been described in detail elsewhere (Strier *et al.*, 2006). We focus on two adult females in the Matão group, which had 81 members during this study period: DD, a grandmother who was carrying an infant when long-term monitoring on this group was initiated in 1982, and is therefore estimated to have been at least 30 years old during the present study; and her daughter, DB, who was born in 1996 and was the third of three natal females (out of 38 natal females that have survived to dispersal age) to remain and reproduce in this group (Martins and Strier, 2004; Strier *et al.*, 2006). DB's first infant, a son, DN, was born in early June 2005.

On 2 September 2005, DD was first seen traveling with her three-month-old grandson (DN) on her back. DD was observed carrying DN on subsequent occasions in 2005. From January to July 2006, instantaneous scan samples (Altmann, 1974) were conducted at 15-minute intervals on all females visible, to assess the proportion of time that DD carried her grandson relative to the proportion of time that he was carried by his mother. At the onset of each scan sample, the females' activities (e.g., resting, traveling, feeding, socializing, drinking water, and undetermined) and all individuals within a five-meter radius were recorded (Strier, 1987). DD and DB were the only females observed carrying DN (i.e., both transporting him while active and resting in contact with him). We calculated the monthly proportion of scan samples in which either DD or DB was carrying or in contact with DN, and in which DB was among her mother's nearest neighbors when DD was carrying or in contact with her grandson. We also examined whether the monthly distribution of both females' activities differed when they were carrying versus not carrying DN. We present descriptive statistics without analyses because of our small sample sizes.

Results

One or both females were observed in 332 of the 2,162 scan samples conducted during the present study period. This resulted in a total of 171 observations of DD (median = 23, range = 6–46, n = 7 months), and 184 observations of DB (median = 23, range = 7–73, n = 7 months). The percentage of monthly observations in which DD was seen carrying her grandson ranged from 0–60.8% (median = 31.1%, n = 7 months), while those in which DB was carrying her son ranged from 4.4–62.5% (median = 12.5%). From April through July, DD carried DN proportionately more often than DB (Fig. 1). DD was rarely in proximity to her daughter during the study period. On average, DB was among her mother's nearest neighbors in 14.4 ± 11.8% of the scan samples when DD was carrying her grandson (median = 18.2%, range: 0–25.0%; n = 6 months) and in 9.6 ± 7.7% of the scan samples in which DD was not carrying him (median = 11.1%, range = 0–17.6%, n = 7 months). Both females exhibited similar activity patterns whether or not they were carrying or in contact with DN. DD was twice as likely to be feeding when not carrying her

grandson, and DB was seven times more likely to be feeding when not carrying her son (Fig. 2).

Discussion

We do not know why DD began carrying her grandson in the first place, or why her care of DN increased during the last four months of the study period. However, neither of the other two females (maternal sisters) that have reproduced in their natal group received any help with carrying from their mother—who, unlike DD, was caring for her own infants when her grandchildren were born. DD's interest in or ability to carry her grandson may have been possible because she was not encumbered with an infant of her own. Based on her reproductive history and the average three-year birth interval (Strier *et al.*, 2006), DD was expected to have conceived during the 2005–06 mating season. Although her last observed copulation was on 2 December 2005, she did not subsequently give birth. Muriquis do not exhibit visible signs of early pregnancy, and the cessation of cycling and mating during the mating season is usually indicative of conception (Strier and Ziegler, 1997, 2005). We do not know, however, whether DD's pregnancy failed, or whether she failed to conceive at all this year. Seven years earlier, during the 1998–1999 mating season, DD also cycled and copulated, but did not subsequently give birth. Her much lower cycling estradiol levels and higher corresponding androgen levels relative to other females that conceived that year were hypothesized to have contributed to her reproductive failure (Strier and Ziegler, 2005). Although she has reproduced in the intervening years, it is possible that during the present study, she experienced similar conception difficulties to those when she was seven years younger.

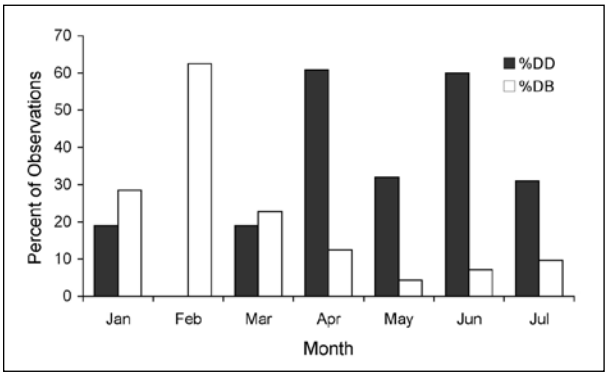

Figure 1. Grandmaternal versus maternal infant-carrying and contact. Percentages are based on scan samples in which DD and DB were carrying or in contact with DN.

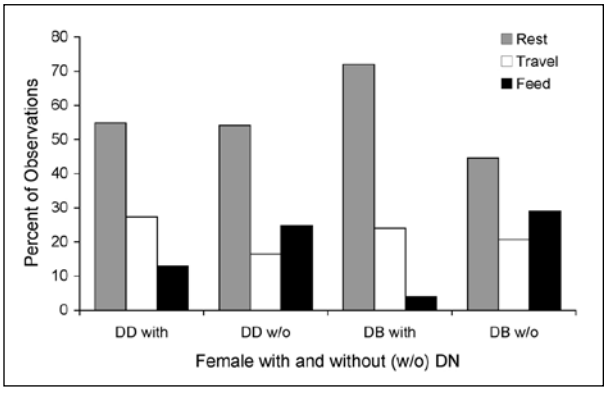

Figure 2. Distribution of DD's and DB's main activities relative to their contact with or without DN. Resting with DN involved physical contact; traveling and feeding with DN involved carrying him.

Although DD and DB were rarely in close proximity, DB was more likely to be among DD's nearest neighbors when DD was carrying her grandson than when she was not. We do not know whether DD initiated proximity with DB to gain access to her grandson, or whether DB initiated proximity with DD to solicit her help or to monitor her while she was carrying DN. Both DD and DB were less likely to feed when they were carrying DN than when they were not. It is tempting to infer that by carrying her grandson, DD liberated her daughter to feed unencumbered, but muriqui mothers often "park" their infants in the canopies of the trees in which they are feeding (Strier, 1999, p. 84). If DN was parked nearby when either his mother or grandmother were feeding, neither was scored as carrying him.

Extended allomaternal care by northern muriquis has previously been observed on only one other occasion during our long-term monitoring of this group, and curiously, the same female (DD) was also involved. On that occasion, DD carried her own and another female's similarly aged infant for 1½ days before relinquishing one of the infants to the other mother. In the process, however, the infants were exchanged, and both mothers successfully weaned and reared their adopted infants (Martins *et al.*, 2007). In the present case, however, DD focused her attention exclusively on her maternal grandson, despite the presence of other infants in the group at the time. Moreover, none of the other adult females, including those that were not carrying infants of their own, were observed carrying or attempting to carry DN. Although we cannot yet assess whether DD's care of her grandson will have any direct or indirect fitness benefits, our observations of persistent investment by a grandmother in her maternal grandson indicate that grandmaternal care can occur within a patrilocal society when a daughter atypically reproduces in her natal group and the grandmother is not carrying an infant of her own.

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Caracterización de la Población del Mono Aullador (*Alouatta palliata palliata*) en el Refugio Nacional de Vida Silvestre Isla San Lucas, Costa Rica

Marta Marleny Rosales-Meda

Introducción

Los estudios realizados con monos aulladores en sitos con aislamiento geográfico se han desarrollado principalmente en las islas de Barro Colorado (Milton 1990), Orquídea (Froehlich y Thorington, 1982, 1992) y Coiba (Milton y Mittermeier, 1977) en Panamá, donde predomina la vegetación de bosque tropical. Dichos estudios han sido de utilidad para conocer la ecología y comportamiento de los aulladores en estos hábitats. Hasta la fecha no existe información acerca del estado de estos primates en ambientes aislados geográficamente, estacionales y reducidos. Este es el caso del Refugio Nacional de Vida Silvestre Isla San Lucas (RNVSISL) en Costa Rica, en donde habita una población introducida de monos aulladores (*Alouatta palliata palliata*) desde hace 40 años (Costa Rica, MINAE, 2005). Se ha reportado que dicha especie juega un papel determinante en la regeneración y restauración de hábitats, principalmente