

## SHORT ARTICLES

### TWINNING IN TITIS (*CALLICEBUS COIMBRAI*): STRETCHING THE LIMITS OF BIPARENTAL INFANT CAREGIVING?

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#### Introduction

Twinning occurs rarely in all anthropoid primates except for the marmosets and tamarins (Callitrichidae). While twin births are the norm in callitrichids, there are only a few recorded cases of twinning from field studies of other platyrrhines, such as *Alouatta* (Chapman and Chapman, 1986; Crockett and Rudran, 1987; Bicca-Marques and Calegari-Marques, 1994), *Aotus azarae* (Huck et al., 2014), *Aotus vociferans* (Aquino et al. 1990), *Ateles belzebuth* (Link et al. 2006), and *Brachyteles hypoxanthus* (Strier, 1991).

In titis (*Callicebus*), only two twin births have been recorded in the wild (Knogge and Heymann, 1995; Lawrence, 2007). In captivity, Valeggia et al. (1999) recorded two twin births in a total of 148 events involving 32 females in a colony of *Callicebus moloch*, which is roughly equivalent to the typical twinning rate in anthropoids. In all these cases, however, one of the titi infants died or disappeared within six months of the birth. The present study reports on the events following a twin birth in a free-ranging group of *Callicebus coimbrai* in eastern Sergipe, Brazil. Only one twin survived to weaning, the typical pattern in titis, suggesting that the energetic constraints of infant carrying in these platyrrhines may limit the potential for the survival of twins in this species.

#### Methods

The records presented here were obtained through the systematic monitoring of a well-habituated *Callicebus coimbrai* study group between May, 2011, and March, 2013 at the Mata do Junco State Wildlife Refuge (10°32'00" S, 37°03'00" W) in the municipality of Capela. At the beginning of the study period, the group contained six members, including a breeding pair, one supernumerary adult, two subadults, and a juvenile of approximately one year of age. Following an initial period of habituation, the group was monitored continuously on four or five consecutive days each month between July 2011 and June 2012, and on most months between July 2012 and March 2013. In addition to scan sampling for the collection of basic behavioral data (Santana, 2012; Souza-Alves, 2013), important events such as social interactions were recorded in all-events fashion (Altmann, 1974).

#### Results

In the first month of habituation (May, 2011), the breeding pair was observed copulating on one occasion, during an interaction that lasted approximately five seconds. During subsequent months, the nonbreeding adult spent long periods in a peripheral position in relation to the study group, and usually only appeared in the vicinity of the other group members when retiring to a sleeping site together. From November onwards, this individual had apparently dispersed from the study group, and was sighted only occasionally during monitoring. On November 22nd, 2011 (mid dry season), the first observation day in this month, the male member of the breeding pair was observed carrying two infants that appeared to be only a few days old. During the subsequent monitoring period (five days), the male carried the infants continually except when they were nursing, when the female carried them, and during two rest periods, when the juvenile was observed with the infants on its back. During subsequent months, the male was invariably observed carrying both infants on its back, except when they were nursing.

On the first day of monitoring in the early rainy season month of April 2012 (April 9th), only one infant was observed being carried by the adult male. The second twin was never seen again. Considering that the infants appeared to be a few days old when first observed on November 22nd, 2011, the individual that disappeared between March 9th (the final day of monitoring in this month) and April 9th would have been between four and five months old, just a little over halfway through the weaning period (Souza-Alves, 2013). The surviving twin was still alive and present in the study group in February 2014 (M. A. Santos, pers. comm.). The cause of the infant's disappearance remains unclear, although the male was observed dropping one of the infants, which fell to the ground, on two occasions, once in January and once in February (R. R. D. Chagas, pers. comm.). A common marmoset (*Callithrix jacchus*) was attacked and killed by a viper (*Bothrops leucurus*) on the ground within the home range of the titi group during the study period (Ferrari and Beltrão-Mendes, 2011), and snakes appear to be relatively common within this area (pers. obs.), although any inference on the possibility of a snake attack would be no more than speculation.

#### Discussion

Twinning in the callitrichids may have evolved in the context of cooperative care-giving behavior (Dunbar, 1988). Ross (1991) concluded that this shift in reproductive output was mediated by a reduction in the relative size of the neonate, which has not occurred in titis. An additional factor here is that, whereas callitrichid groups typically contain multiple caregivers, which may contribute significantly to reproductive success (Goldizen, 1987; Snowdon, 1996; Heymann, 2000), infant carrying in titis is normally the sole responsibility of the father (Wright, 2013). Assuming

that this behavior has evolved in response to the energetic demands of reproduction on the female in these small monkeys, or alternatively, as a strategy to maintain a comparatively short birth interval (Garber and Leigh, 1997), the double burden of twins may be especially onerous for the father.

While the data are still scant, a pattern does appear to be emerging. In all three recorded cases in free-ranging titis, one of the infants disappeared within the first few months following the birth. In *C. cupreus*, the infant disappeared at 1–2 months of age (Knogge and Heymann, 1995), whereas in *C. brunneus*, the disappearance occurred at around five months (Lawrence, 2007), as in the present study. In all three cases, the remaining twin survived at least until weaning. In captivity, the two twin births observed in *C. moloch* each resulted in the loss of one of the infants shortly after birth (Valeggia et al., 1999). There is, however, one unusual case of an adoption in a *Callicebus nigrinus* group (Cäsar and Young, 2008), where the breeding pair cared for, and raised two infants simultaneously, although rearing success may have been mediated by factors such as the different ages of the infants and the fact that only one of them was reared throughout the whole weaning period. A remarkably similar pattern has been recorded in Azara's owl monkey (*Aotus azarae*), a species similar to titis in body size (adult weight ca. 1 kg: Fernandez-Duque et al., 2013) and the caregiving behavior of the breeding male, which is the primary infant carrier. In the two recorded cases of twinning in a wild *A. azarae* population in northern Argentina (Huck et al., 2014), one of the infants disappeared from one set of twins at approximately three months of age, and from the other at five months. In each of these two cases, the remaining twin survived past weaning. In the much larger-bodied atelids (female body weights of over 5 kg: Rylands and Mittermeier, 2013), by contrast, the survival of both twins appears to be the norm, despite the fact that only the mother carries the infant in these species. Even so, rearing twins has high energetic costs for the mother, and retards growth and development in the infants (Chapman and Chapman, 1986; Link et al. 2006).

The sum of the evidence thus appears to indicate that energetic constraints on reproduction in the small-bodied monogamous platyrrhines (*Aotus* and *Callicebus*) limit the potential for the rearing of twin infants. This also reinforces the conclusion that twinning in the smaller-bodied callitrichids is mediated by a set of factors (Tardif, 1994), including the reduced size of the neonate and caregiving by nonbreeding group members (which in turn is mediated, in part, by the suppression of ovulation in subordinate adult females, in most cases: Digby et al., 2011). The social groups of the strictly monogamous titis and owl monkeys normally contain no supernumerary adults, and immature group members are rarely if ever seen carrying infants. In the present study, as in the other cases of both *Callicebus* and *Aotus*, the presence of twins in the group did not affect the caregiving behavior of the mother noticeably, in other

words, the mother only took the infants to nurse them. In most cases one twin disappeared after a few months of life, rather than shortly after the birth, supporting the conclusion that the increasing energetic onus of infant-carrying on the father contributed to the eventual loss of one of the twins. This may imply a decreasing ability to retrieve fallen infants from the ground, for example, although there is no direct evidence for the cause of any disappearance. These conclusions also reinforce the importance of the contribution of supernumerary caregivers in the much smaller-bodied callitrichids to guarantee the survival of both twins.

## Acknowledgements

MMS and JPSA are grateful to CAPES for graduate stipends, and JPSA and SFF to CNPq for research grants. JPSA also thanks the International Primatological Society for financial support. We are also grateful to SEMARH/SE and CPB/ICMBio, and Jessica Lynch Alfaro and Maren Huck for their helpful suggestions and advice.

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## INFANTICIDES DURING PERIODS OF SOCIAL STABILITY: KINSHIP, RESUMPTION OF OVARIAN CYCLING, AND MATING ACCESS IN WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS*)

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### Introduction

In non-human primates, most infanticide cases (85%) occur during periods of social instability when a change-over of the top-ranking male occurs (van Schaik, 2000). In contrast, infanticides during periods of social stability have only been reported for a few species (Valderrama *et al.*, 1990; Murray *et al.*, 2007; Gibson *et al.*, 2008). The sexually selected infanticide (SSI) hypothesis (Hrdy 1974, 1979), proposes that infanticide is a male reproductive strategy in that males adopting this strategy benefit by gaining mating access to females who resume ovarian cycling prematurely following the death of their unweaned offspring. According to the SSI hypothesis, infanticide is a male reproductive strategy if: 1) the attacker is unrelated to the infant, 2) the mother's time to conception is shortened by the infant's death, and 3) the infanticidal male has an increased probability of siring the mother's future offspring. Though other hypotheses have been suggested to explain infanticide, most reported cases occur during or after periods of social instability and thus appear to fit the SSI hypothesis (Hrdy 1974, 1979; van Schaik, 2000).

In white-faced capuchins (*Cebus capucinus*), infanticides are commonplace during periods of social upheaval resulting