

Double infanticide in a free-ranging group of buffy-headed marmosets, *Callithrix flaviceps*

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Abstract This study describes two infanticides in a free-ranging group of *Callithrix flaviceps*. In November 2008, four females gave birth within a period of approximately 10 days. On the day after the third birth, the new mother was attacked by an unidentified individual, resulting in the death of one of her infants due to a bite to the top of the head. Five days later, the fourth female gave birth to twins, and the next day, the more socially dominant of the breeding females was observed ingesting the head of one of these infants. All other infants survived until the end of the study. With the exception of the unusual number of births and attacks, the behaviour appeared typical of that recorded in other marmosets, where socially dominant breeding females attack the offspring of subordinates, apparently as a strategy aimed at reducing competition for the services of infant caregivers.

Keywords *Callithrix flaviceps* · Polygyny · Infanticide · Cannibalism · Reproductive strategies

Introduction

Infanticide occurs in many nonhuman primates, although it depends on specific socio-ecological circumstances, and

has been observed in a small number of field studies. The classic example is the elimination of unrelated offspring by polygynous males as they take over a harem (van Schaik and Janson 2000), a pattern also seen in other mammals, such as lions, *Panthera leo* (Packer and Pusey 1983). This is also the typical pattern in large-bodied platyrrhines, such as *Alouatta* (Galetti et al. 1994) and *Cebus* (Ramirez-Llorens et al. 2008).

In the small-bodied marmosets (*Callithrix* spp.), however, infanticide is related primarily to competition among breeding females (Digby 2000), a pattern observed in some other cooperatively breeding mammals, such as meerkats, *Suricata suricatta* (Clutton-Brock et al. 1998). Typically, the behaviour is perpetrated by one breeding female against the offspring of a second female, which is often known or assumed to be related (Digby and Saltzman 2009). This relatedness constitutes an additional difference in comparison with the typical male pattern.

Infanticide has now been well documented in the common marmoset, *Callithrix jacchus*, including at least seven records in free-ranging groups (Digby 1995; Roda and Pontes 1998; Lazaro-Perea et al. 2000; Melo et al. 2003; Sousa et al. 2005; Bezerra et al. 2007). The lack of records for other marmoset species may be a sampling artefact, in addition to the fact that the presence of multiple breeding females is likely a prerequisite for the behaviour (see Digby and Saltzman 2009). The present report on infanticide in the poorly known *Callithrix flaviceps* confirms this conclusion. This is not only the first report of the behaviour in this species, but also the first case involving the offspring of two different females in a free-ranging marmoset group. Otherwise, the circumstances, behaviour patterns and apparent strategies involved are similar to those in *C. jacchus*.

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Fig. 1 Tenure of individuals in the group. Infanticides are marked with *arrows*. The infants born in November 2008 could not be distinguished and were denominated by IF + name of the mother

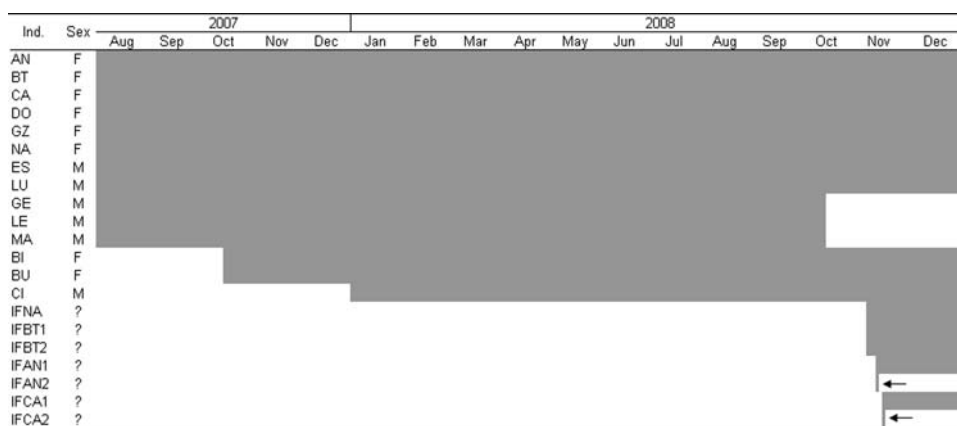


Table 1 Records of births in the *C. flaviceps* study group

Female	Date	Litter	Details
BT	17–20/12/2007 ^a	Twins	Both infants survived until the end of the study
CA	~31/12/2007 ^a	Singleton	Survived until the end of the study
BT	9–12/11/2008 ^a	Twins	Both infants survived until the end of the study
NA	9–12/11/2008 ^a	Singleton	First seen on 14/11/2008, estimated age 4 days. Survived until the end of the study
AN	15/11/2008	Twins	One twin victim of infanticide on 16/11/2008. The other survived until the end of the study
CA	20/11/2008	Twins	One twin victim of infanticide on 21/11/2008. The other survived until the end of the study

^a Approximate dates based on estimated age of infants when first sighted in the group

Study area

The study took place in the Augusto Ruschi Biological Reserve (19°52'S, 40°33'W) in the Brazilian state of Espírito Santo, which encompasses 3,589 ha of Atlantic Forest. Buffy-headed marmosets, *Callithrix flaviceps*, occur at relatively low densities within the reserve (Hilário 2009).

Materials and methods

One of us (R.R.H.) monitored the study group between October 2007 and December 2008. During habituation, in 2007, all adults and sub-adults were identified individually on the basis of natural variation in the pelage and marks such as scars, and all subjects were fully habituated to the presence of researchers, allowing observation from close quarters. Basic behavioural data were collected in scan samples (1-min scan at 5-min intervals: Ferrari and Rylands 1994) conducted continuously throughout the day on 6–9 days each month between January and December, 2008 (958 contact hours). Social dominance was established from an analysis of all-events records of agonistic interactions and food sharing (Hilário 2009). Additional data were collected ad libitum.

Results

Group composition and births

General behaviour patterns were similar to those observed in other studies of *C. flaviceps* (Ferrari 1991; Guimarães 1998). The group contained 11–16 members during the course of the study period, including at least two and up to six adults of each sex (Fig. 1). One of the females (GZ) was socially dominant over all other group members, but did not reproduce. Of the other adult females, one (BT) was dominant over the others, and gave birth at the end of 2007, together with a second female, CA (Table 1). In October 2008, three adult males emigrated together from the study group. Less than 1 month later, three females (BT, NA and AN) all gave birth within the second week of November (Table 1). Five days later, CA also gave birth to twins.

First infanticide

The first infanticide occurred at 09:40 h on the day after the third birth. At this moment, an unidentified adult grappled with AN, who was carrying both her twins, and the two animals fell to the ground together from a height of approximately 2.5 m. In response to AN's alarm vocalizations, other group members approached emitting excited

“tsik” calls. After less than 20 s, the animals stopped grappling and moved away quickly, leaving one of the infants on the ground.

The female GZ and the adult male ES approached the fallen infant, and began to sniff, touch and lick it. The female CA approached, but was threatened by ES with “erh-erh” vocalizations and withdrew. Other group members observed in obvious distress from distances of 1–5 m. After 10 min, GZ placed the infant on her back and climbed up to a branch 3 m above the ground. Two subadults (BI and CI) and ES approached GZ to inspect the infant, while other individuals continued to observe from a distance.

By 10:05 h, the group moved on, but 1 h later, 100 m from the site of the attack, long calls were emitted and some individuals gathered round GZ and ES, which were on the ground touching the infant, now barely moving and already too weak to cling to GZ’s back. The hand of GZ was smeared with blood. A second adult female (DO) then began to smell, touch and lick the infant. This continued for about 15 min, when DO and ES moved away. At 11:40 h, the infant’s mother (AN) approached GZ and the infant, which was attracting flies. This appeared to irritate GZ, who tried to keep the flies away from the infant’s body.

After almost 15 min touching, sniffing and licking the infant, AN moved 10 m away and began suckling her other infant. All other group members, except GZ, had now moved out of sight, and she moved away only at 12:07 h, while AN remained in the same position, still suckling her infant. At this moment, it was possible to inspect the fallen infant, which was cold to the touch, but still breathing and vocalizing faintly. There was a deep bite mark on the top of its head, where the aggressor had apparently pierced the cranium with its canines.

The females AN and GZ moved away after 12:30 h to join the rest of the group. These two females remained in close proximity to one another for most of the rest of the day, which was typical of these two individuals (Hilário 2009). At the end of the day, they slept together in a roost 12 m from the rest of the group. On the next evening, two subgroups (the members of which could not be identified) roosted in the same tree but 3 m apart, and on the following night, AN and GZ once again slept together in a separate roost. Previously, the group had roosted in separate subgroups on only two occasions on 105 nights.

Second infanticide

The final birth occurred 4 days later. Between 15:15 and 15:20 h on the following day, contact was lost due to heavy rain, but the group was located through mobbing vocalizations, similar to those recorded during the first infanticide. At 15:37 h, the female BT was observed on a tall

branch holding an infant in both hands and eating its head. The female CA was extremely agitated, twittering constantly and carrying only one infant. One of BT’s 1-year-old daughters was following her mother, as though trying to reach the dead infant.

The other members of the group had grown calm by this time, and had stopped vocalizing. When BT finished ingesting the infant’s head, she discarded the body, which fell to the ground. At this moment, the other group members moved on.

While she eventually grew calmer, CA remained in an agitated state until the end of the day, and waited for more than 20 min after other group members had roosted before retiring. As before, the victim’s mother slept with GZ in a roost separate from the rest of the group. Once these females had roosted, some other individuals moved from the main group to join them. On the next day, the group dispersed over a wide area, and used at least two different roosts 50 m apart.

All five surviving November infants were still alive in December, and remained in the group until the end of the study, when they were a month old. Behaviour was ostensibly normal, and adults cared for infants cooperatively. As each subordinate female was left with only a single offspring, it was possible to confirm that they carried the offspring of other females, given that they were sometimes seen with two infants. It was not possible to tell whether BT engaged in alloparenting behaviour, however.

Discussion

While the perpetrator of the first infanticide was not identified, four individuals can be discounted: GZ, ES and DO, who attempted to rescue the infant, and NA, who was not near the attack. Of the other three adults in the group at the time, the male is an unlikely candidate, CA was at the end of her gestation and BT was still carrying her own newborn twins. The fact that BT was socially dominant and perpetrated the subsequent infanticide makes her the most likely candidate, but this evidence is inconclusive.

The timing of births may be a decisive factor in most cases. As infant caregivers constitute an important resource for callitrichid breeding females (Terborgh and Goldizen 1985), the presence of additional infants obviously reduces its availability. In the present case, the occurrence of seven births within a 10-day period implies that potential competition for caregivers was abnormally intense.

An additional question is why only two infanticides were committed, when other infants remained in the group. Pre-emptive behaviour such as roosting separately may have reduced the risk of further attacks, and mothers may have been more agile when carrying a single infant, and

thus more able to avoid attacks. From a broader perspective, assuming the females are closely related, the perpetrator's motivation may have been mediated by both proximate (familiarity) and ultimate (inclusive fitness) factors. As infanticide is generally limited to a single victim from each litter, even in captivity (Kirkpatrick-Tanner et al. 1996; Bardi et al. 1998), there may be a specific control mechanism.

All previous infanticides in free-ranging marmosets were perpetrated by pregnant females (Digby and Saltzman 2009), so this is the first report for a post-partum female. Saltzman and Abbott (2005) attribute the absence of infanticide in post-partum *C. jacchus* females to (1) a lack of cues for the recognition of their own infants or (2) inhibition of aggression by the hormones that stimulate care-giving behaviour. The former factor would have been irrelevant here, given that all infants were being carried exclusively by their mothers when the infanticides occurred. Any hormonal mechanism may have been outweighed by the abnormal concentration of parous females in the group.

Cannibalism is a component of around half the infanticides in marmosets (Bezerra et al. 2007), although its motivation is unclear. If this were nutritional—as suggested by Melo et al. 2003—it is unclear why the perpetrator typically ingests only the head. It seems more likely that the perpetrator engages in a typical attack on a prey animal, biting first at the head to subdue the victim. Presumably, it may then ingest part of the head either incidentally or instinctively.

While literally dozens of behavioural field studies involving all six callitrichid genera are now available (Digby et al. 2007), infanticide has only been recorded in the wild in *C. jacchus*, *Saguinus fuscicollis* (Tirado-Herrera et al. 2000) and, now, *C. flaviceps*. It seems unlikely that this behaviour is restricted to these species, given that De Vleeschouwer et al. (2001) and Price and McGrew (1991) have recorded it in captive *Leontopithecus rosalia* and *Saguinus oedipus*, respectively, but it is dependent on specific prerequisites, such as the presence of multiple breeding females, and the timing of births. Given this, the large number of records for *C. jacchus* may simply reflect the number of field studies of this species, the presence of two breeding females in many groups and pronounced birth peaks (Digby and Saltzman 2009).

Polygyny appears to be less common in other callitrichids, although it has been recorded in free-ranging *L. rosalia* and three species of *Saguinus* (Smith et al. 2001). Rather than being the norm, as in some populations of *C. jacchus* and possibly *C. flaviceps*, Dietz and Baker (1993) recorded multiple breeding females in only 10% of *L. rosalia* groups. In most cases (but not all; Calegario-Marques et al. 1995; Goldizen et al. 1996), subordinate

females not only give birth to fewer offspring, but the survival rate of these infants tends to be lower than that of dominant females. Given the observations in *C. jacchus* and *C. flaviceps*, it would seem reasonable to assume that, in at least some of these cases, the disappearance of the offspring of subordinate females has been due to infanticide.

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