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Comments/Reflections

An observation of intergroup infanticide in grey-cheeked mangabeys (*Lophocebus albigena*)

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Abstract

In primates, infanticide is occasionally observed during intergroup conflicts but does not fit the predictions of the sexual selection hypothesis. I report an observation of an intergroup infanticide during a sub-group foray in grey-cheeked mangabeys (*Lophocebus albigena*) at the Ngogo site in Kibale National Park, Uganda. Intergroup infanticide appears to be a form of extreme and long-term food defence across primate species, and occurs in conjunction with other forms of food defence.

Keywords

feeding competition, sexual selection, between-group contest, *Lophocebus ugandae*.

1. Introduction

Intragroup infanticide is widely documented across the Primate order (van Schaik, 2000). Infanticidal males improve their own reproductive success by terminating a female's reproductive investment in her current offspring, but these events occur under very specific conditions: i.e., when the infanticidal male is not a potential sire of the infant; the death of the infant hastens the female's return to fecundity; and the male's odds of mating with the newly fertile female improve, either because of his recent immigration or a rise in

rank within the dominance hierarchy (Trivers, 1972). Similarly, infanticides during intergroup conflicts may also benefit male reproductive success when they occur in populations where females disperse multiple times across the lifespan. After an infanticidal attack by an outside male, the female tends to leave the group, either in search of a group with a lower rate of attacks (Teichroeb et al., 2009) or because the resident male's inability to protect the current infant bodes poorly for any future offspring they produce together (Watts, 1989; Steenbeek, 2000); the female will sometimes even join the infanticidal male, who has presumably demonstrated superior competitive ability.

Across primate species, intergroup infanticide is documented far less often than intragroup infanticide, particularly in populations characterized by female philopatry and male dispersal (Shopland, 1982; Harris & Monfort, 2003; Vogel & Fuentes-Jimenez, 2006; Cords & Fuller, 2010), or where females exhibit primary but not secondary dispersal (Watts et al., 2002). In these cases, the infanticidal male makes no effort to join the group or mate with the female when she returns to oestrus, and thus there is no clear improvement in his immediate reproductive success. Instead, these incidents appear to function as a means of intergroup intimidation and may result in avoidance of the competitively dominant aggressor's group. This dynamic leads to the preferential use of space and resources by the aggressor's group (Harris & Monfort, 2003; Mitani et al., 2010), which likely translates into improved fitness over longer periods. Here, I describe an instance of intergroup infanticide in grey-cheeked mangabeys (*Lophocebus albigena*), a primate species characterized by female philopatry and multi-male groups (Olupot & Waser, 2013), in which infanticide has not been previously documented (Arlet et al., 2014).

Neighbouring pairs of grey-cheeked mangabey groups share ~30% of their home ranges (Brown, 2013), providing many opportunities for intergroup conflict, and do not defend clear territorial boundaries (cf. description in Cords, 2002). However, groups only come within close range of each other under limited conditions (Brown & Waser 2018). Groups engage in two types of conflict: whole-group encounters, in which the entirety of two groups are in close proximity; and sub-group forays, in which only one or a few individuals of a group travel several hundred meters toward a neighbouring group (Brown, 2013). Aggression during these encounters takes the form

of chasing and physical attacks. Aggression during whole-group encounters functions to maintain or acquire access to important feeding sites, but the function of sub-group forays remains unclear. Most intergroup encounters are aggressive, and while adult males participate in all such encounters, females participate far less often and only if males also exhibit aggression. Females with unweaned infants position themselves at the rear of their group during an encounter, as far as possible from the opposing group while remaining in visual contact with group-mates (Brown, 2011). Mothers remain highly vigilant and agitated during these encounters and are always closely accompanied by an adult male, who I suspect may be the sire.

Grey-cheeked mangabeys are not seasonal breeders (Arlet et al., 2015) and groups rarely have >1 female with a maximally inflated sexual swelling (Brown & Waser, 2018). Females mate with multiple males of varying ranks during each cycle (Arlet et al., 2007), but there are no reports of extra-group copulations during intergroup encounters, or other mating attempts with males residing in other groups. Females give birth every approx. 2.8 years (Arlet et al., 2015) and 40% of infants die or disappear before reaching independence, largely due to illness, predation by chimpanzees, and accidental falls during male–male fights (Arlet et al., 2014). Of those infants that do not reach weaning age, 43% disappeared for unknown reasons but most of these disappearances occurred shortly after male immigration events, which seem to trigger high frequencies of male-male fights and accidental falls by infants. There are no reports of males stalking or harassing females with unweaned infants (cf. Borries, 1997).

2. Methods

With the aid of a team of field assistants, I studied intergroup conflicts (whole-group encounters: $N = 41$; sub-group forays: $N = 34$) among eight habituated groups of grey-cheeked mangabeys at the Ngogo research site in Kibale National Park in western Uganda from January 2008 through March 2009 (8736 observation hours; Brown, 2011). We followed 3–6 groups per day from dawn to dusk, noting group composition daily and recording group location every 10 min. We recorded other behaviour, including long-distance vocalizations and copulations, as it occurred. Observers were distributed throughout the focal group to maximize the detection of an approaching neighbour, and during an intergroup encounter all observers focused their

attention on the details of the interaction. We recorded the number of infants and adult males in each group every day. There were 23 unweaned infants present at various points during this study, of which one was the victim of this observed infanticide.

3. Results

The incident occurred on 12 February 2008, during a follow of the M1 group. At 15:20, I was positioned south (in front) of the focal group with a visitor while one field assistant was at the northern (rear) edge and the second assistant was in the centre of the group. Many individuals in the group began vocalizing loudly, producing screams and staccato barks, when an adult male entered the group from the north. There was an intense fight, from which the intruder male escaped by running on the ground directly toward me. The male had one of the group's two infants in his mouth, which was screaming but not moving; I suspect the infant was paralyzed and that the male had bitten down on its spine. The male did not appear to see me until he was ~3 m away, at which point he climbed a small understory tree, travelled directly over my head, and continued moving south and up into the upper canopy. He was not followed by any members of the M1 group. Soon after reaching the upper canopy, the infant stopped screaming. I lost sight of the male for a few minutes and after finding him again, discovered that he no longer had the infant. Though two observers searched for several hours, they were unable to find the infant, nor was it present with the group in the days and months following the attack. Two other observers followed the male, who returned to his group shortly afterward. We identified him on the basis of unique physical characteristics as a resident of the M5 group (which we were not following that week), whose home range was immediately north of the M1 group. Neither in the following six observation days that month, nor in subsequent observation periods (generally 1 week long and separated by gaps of 10–14 days), did we observe this male attempting to join the M1 group or to mate with the mother of the infant.

The infanticidal attack occurred within the core area (50% kernel density polygon) of the M1 home range and outside the M5 range. M1 had been moving south (away from the M5 range) that day but after the attack it remained stationary until dusk. On the following day (13 February) it moved north and ranged within the area of overlap with the M5 home range, and

returned to this area again on 15 February; in other words, the victim's group did not avoid the attacker's group immediately after the encounter. However, in the subsequent 13 months of the study, the victim's group used the shared overlap area less than expected, based on the size of this area relative to the size of the home range, and the attacker's group used it more than expected (Brown & Gaffney, data not shown). Because the attack occurred early in the study, it is unclear whether it caused a shift in the home ranges of the two groups.

4. Discussion

I observed one infanticide during a sub-group encounter in the course of this 15-month study. Infanticides are generally infrequent events in primate groups (Hrdy, 1979; van Schaik, 2000), and those that occur during intergroup conflicts are particularly rare (e.g., Watts et al., 2002; Harris, 2006; Vogel & Fuentes-Jimenez, 2006). Despite the rarity of infanticide in grey-cheeked mangabeys, the behaviour of both males and females during all intergroup encounters indicates that it is perceived as a substantial threat. As is the case with predation (Isbell, 1994), the threat of harm may be far more pervasive than actual events but nonetheless be sufficiently strong to shape behavioural responses. When infanticide is a recurring risk during intergroup conflicts, females with unweaned infants should avoid contact with the opposing group and may even position themselves at the rear of their group.

As seen here with grey-cheeked mangabeys, several other species also target immatures specifically during sub-group forays (western black-and-white colobus, Korstjens et al., 2005; chimpanzees, Mitani et al., 2010; ursine colobus, Sicotte & MacIntosh, 2004). However, not all intergroup infanticide occurs in the context of sub-group forays: in species lacking this form of intergroup interaction, infants are attacked during whole-group conflicts (Shopland, 1982; Agoramoorthy & Rudran, 1995; Harris & Monfort, 2003; Vogel & Fuentes-Jimenez, 2006; Cords & Fuller, 2010). It is unclear what social or ecological conditions cause certain species to make sub-group forays but not others.

In general, aggression directed at adults in the opposing group is often a means of acquiring immediate access to feeding areas during an intergroup conflict (Harris, 2007). In contrast, infanticidal aggression may be a way

of intimidating neighbouring groups to create a ‘landscape of fear’; i.e., a means of ensuring priority of access to food resources for the infanticidal group in shared areas (Agoramoorthy & Rudran, 1995; Harris & Monfort, 2003; Mitani et al., 2010). A male who kills neighbours’ infants may accrue intragroup benefits, such as greater resources for existing offspring through territorial expansion. In sum, intergroup infanticide appears to be an extreme and unusual form of feeding competition.

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