

Case Study:

Aggressive Intergroup Encounter and Infanticide in the White-thighed Colobus (*Colobus vellerosus*) at Kikélé Sacred Forest, Bénin

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INTRODUCTION

In nonhuman primates, there is tremendous variation in intergroup relationships, from affiliative to neutral to lethal and which sex predominantly participates in intergroup encounters (IGEs) (van Belle 2015; Koch *et al.* 2016; Scarry 2017; Furuichi 2019, van Belle *et al.* 2020). Female primates may participate in food resource defense. Measuring how much fitness that an individual gains through food defense is difficult, however. For this reason, the degree of female participation in resource defense and the proximity to such food resources are often used as proxies (Scarry 2017).

Colobus species are known to behave aggressively during IGEs (*Colobus angolensis*: Bocian 1997; *Colobus guereza*: Fashing 2001; Harris 2006; *Colobus vellerosus*: Sicotte & Macintosh 2004; Teichroeb *et al.* 2012; Teichroeb & Sicotte 2018; *Colobus polykomos*: Dasilva 1989; Korstjens *et al.* 2005). In these species, males behave aggressively to directly defend mates but also to defend critical or high-quality food patches (Fashing 2001; Sicotte & Macintosh 2004; Harris 2006; Teichroeb *et al.* 2012; Teichroeb & Sicotte 2018). Sicotte's group at the University of Calgary (Canada) has extensively examined male and female behavior during IGEs in the white-thighed colobus (*C. vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana. According to their reports, there is strong support for male mate defense and resource defense, while female resource defense occurs only occasionally (Sicotte & MacIntosh 2004; Sicotte *et al.* 2007; Teichroeb *et al.* 2012; Teichroeb & Sicotte 2018).

In contrast, in *C. polykomos* female participation in IGEs was substantial in Tiwai Island Primate Sanctuary in Sierra Leone (Dasilva 1989) and Tai Forest, Côte d'Ivoire (Korstjens *et al.* 2005). Here we report an aggressive IGE that occurred between two groups of *C. vellerosus* at Kikélé Sacred Forest (KSF) in northwestern Benin that resulted in infanticide. Infanticide by males and male attacks on infants have been previously reported in *C. vellerosus* at BFMS (Teichroeb & Sicotte 2008). Our intent here is to describe our observation as a case study to examine how it compares with other reports.

METHODS

Study area and study subjects

This study took place at Kikélé Sacred Forest (KSF) (19.8 ha, 9.009° N, 1.729° E) (Figure 1). The KSF is a Guinéo-Soudanien dry semi-deciduous forest characterized by demarcated seasons, a long wet season (April–October), and a short dry season (November–March). The rainfall is 1,200–1,300 mm per annum (Djogo-Djossou *et al.* 2012). KSF has been protecting *C. vellerosus* as the village's totem for centuries. Most, if not all, Kikélé villagers revere the monkeys and do not hunt them, but when the monkeys enter into adjacent gallery forests, they may be shot. During the last several decades, the Kikélé population of this species has dwindled due to habitat reduction and hunting in neighboring areas. At present, there remain two groups, one containing 19 individuals and another containing two.

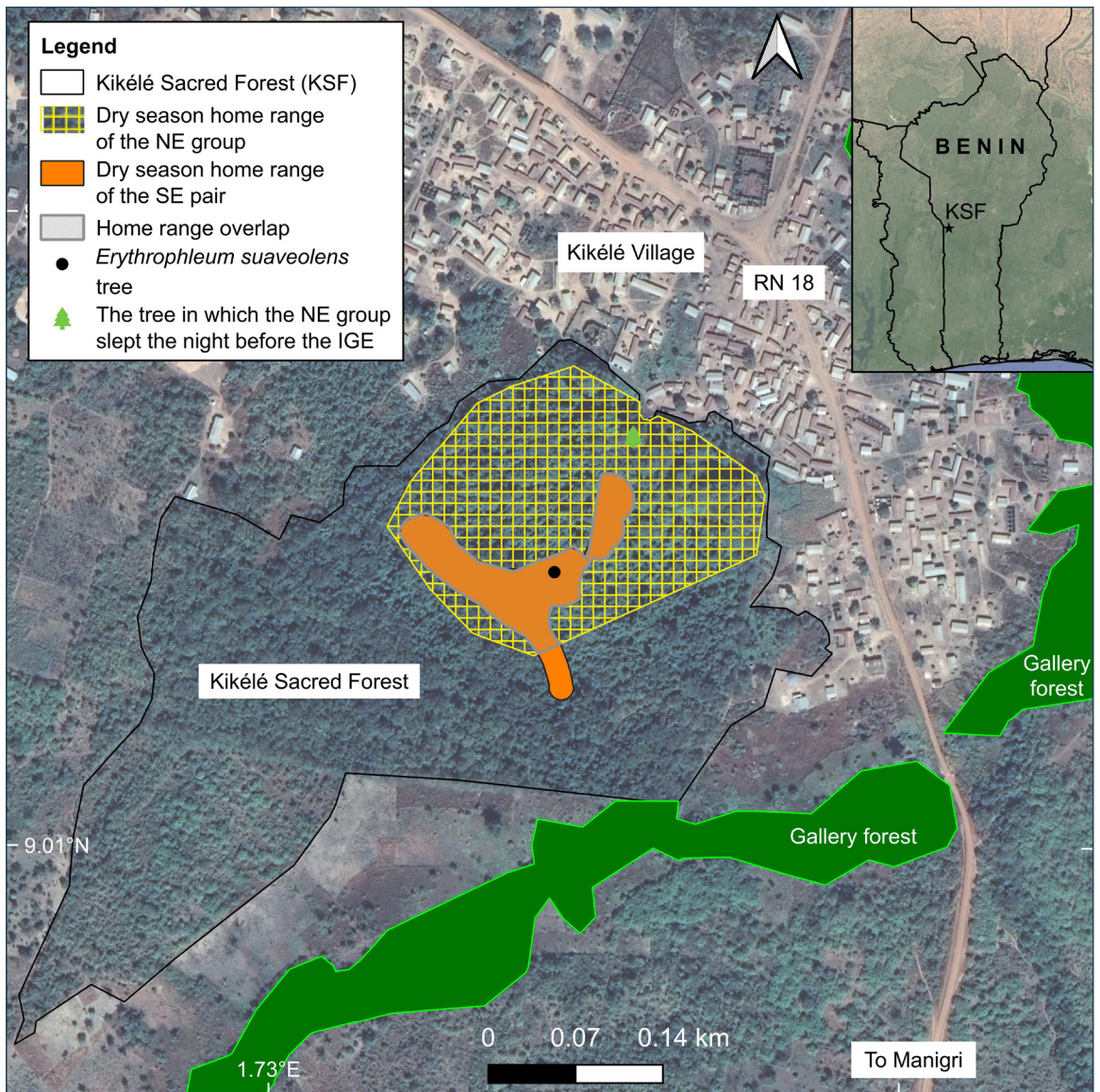


Figure 1. Kikélé Sacred Forest in the Republic of Bénin shown with the dry season home ranges of the NE group and the SE pair.

The subjects of our study were 19 members of the NE group (focal group) (2 adult males, seven adult females, two subadult males, five subadult females, two juveniles, and one infant) (this group was mixed with four mona monkeys, *Cercopithecus mona*); and the SE group (SE pair) containing one adult male and one adult female. Many, but not all, members of the focal group are habituated to human observers. The adult males of the focal group are Esaka (Figure 2), an older male, and Marc. One of the seven adult females of the NE group is Mouli who had a two-month-old white infant, Celi. In *C. vellerosus*, newborns are born with the white pelage, which

gradually changes into the adult pelage pattern by about three months of age.

The adult male of the SE pair is Mouka and the female of the SE pair appeared to be nulliparous. Intragroup contest competition is rare in the focal group. Male incursion can be defined as a behavior in which an adult male encroaches on another group's home range within 10-m proximity of another group. In nine months of this study, incursions by the two NE adult males occurred only six times. Five of these incursions occurred after the infanticidal episode. The violent episode reported here is the only aggressive IGE observed during the study period.

Data collection and spatial data analysis

RCO collected behavioral and spatial data, dawn to dusk, as part of a larger behavioral-ecology study of the focal group between July 2017 and March 2018. Data were collected using scan sampling at 15-minute intervals. Each scan lasted about two minutes. The location of the center of the focal group was recorded using a Garmin GPSMap 62ST device. The SE pair was also followed occasionally, but not systematically, guided by Mouka's loud calls. On January 20, 2018, the day of the reported incident, the focal group was followed. When Esaka began foraging towards the SE pair, the behavior of observable group members was recorded *ad libitum*. After the occurrence of the IGE, the focal

group was followed on January 21, 24-28, and 30. The spatial analysis of the focal group's movements (e.g., daily path length estimation, home range size determination, home range overlap estimation) was done with QGIS 3.12. During the dry season, 94.3% of the SE pair's home range belonged to the NE group's home range (Figure 1); however, because the SE pair was not consistently followed, its true home range area and size are unknown.

Observation

At 6:32 on January 20, 2018, the NE group members were spread out on two large trees, *Holoptelea grandis* (Ulmaceae) and *Ficus congensis* (Moraceae), adjacent to the village where they

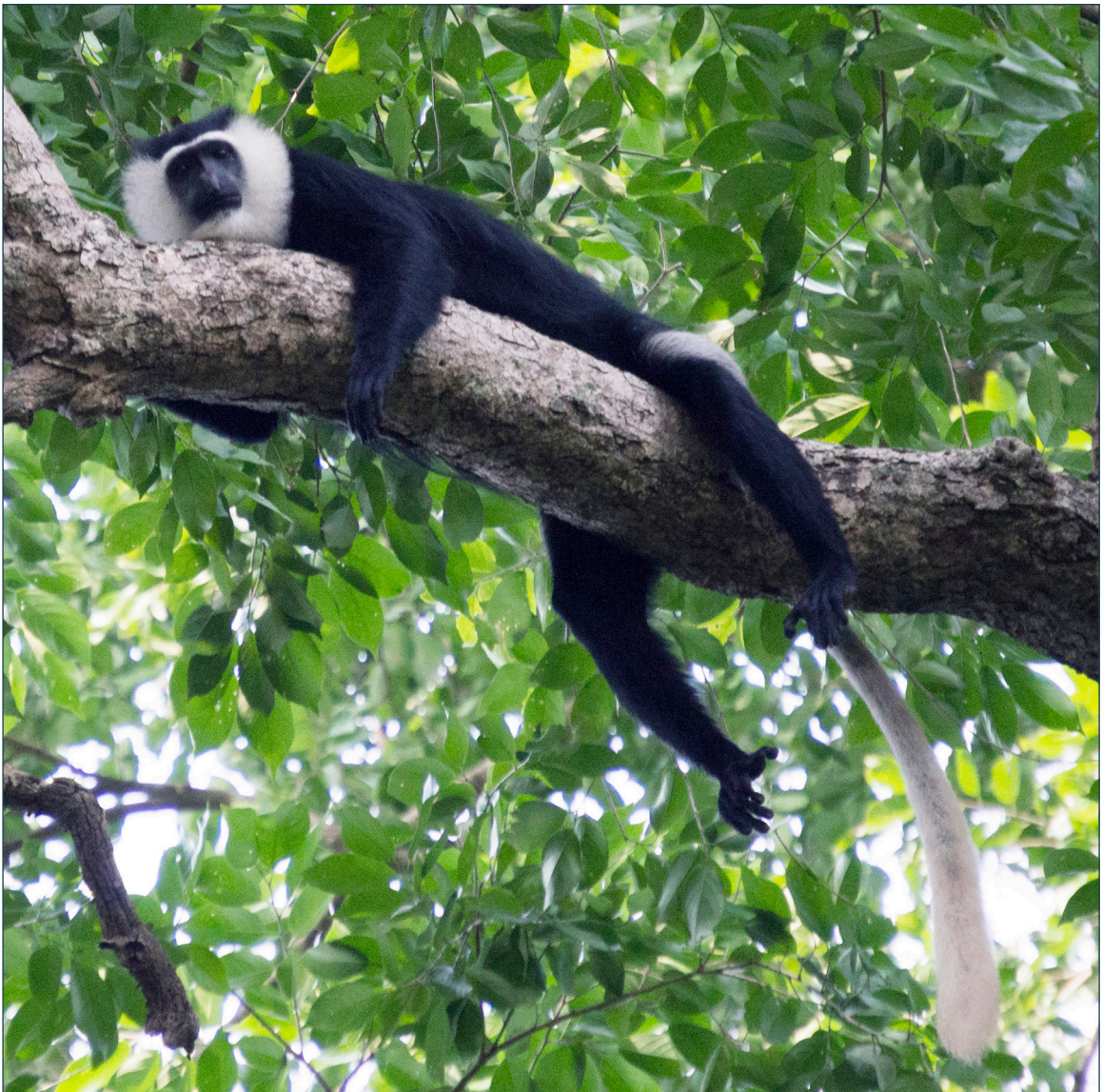


Figure 2. Esaka, the older adult male of the NE group in Kikélé Sacred Forest. Photograph by R. Matsuda Goodwin.

slept the night before (Figure 1). This is one of the sleeping sites within the group's home range. In the early morning, they woke slowly and began feeding on the leaf buds, flower buds, flowers and young leaves of *H. grandis* and *F. congensis*. At 8:45, Esaka of the focal group gave loud calls. Mouka, the adult male of the SE pair, which was about 150 m south of the position of the NE group, gave a loud call immediately following Esaka's vocalization. After moving about 15 m southwest, the NE group began feeding on the buds and young leaves of *H. grandis* and *Celtis integrifolia* (Cannabaceae) until 10:15. The incident began at 10:15 and ended at 10:22.

At 10:15, the NE group started moving about 120 m south into the SE pair's area. The pair was feeding on the young leaves of a large but rare tree of *Erythrophleum suaveolens* (Leguminosae) (Figure 1). This tree is located in the area where the two groups' home ranges overlap. The white-thighed colobus preferred to feed on the young leaves of this tree in January 2018.

Esaka was at the front of the group as the NE group members were moving into the area. He forayed directly towards the SE pair in the *E. suaveolens* tree. Then, the two groups met at a large tree of *Cassia* sp. (Leguminosae) immediately west of the *E. suaveolens* tree. As soon as the focal group members reached this tree, several adult females, Esaka, and Marc began chasing the SE pair, but Mouka (the adult male of the SE pair) quickly ran towards Mouli, a female in the focal group. Mouli was carrying Celi on her ventrum. Then, Mouka ran after Mouli. He attempted to pull Celi off of Mouli's ventrum, but what happened next is not clear due to commotion surrounding Mouli. She fled to another tree, screaming, still in possession of the infant. No wound or blood was visible on the body of the white infant, but it was limp in Mouli's hands. Now, all the NE members chased the SE pair to another tree, while many individuals vocalized. As Mouka moved toward a female in the NE group, one of the adult females of the NE group bit the SE female on the neck; she tumbled from the tree, screaming. Esaka bit Mouka on the back several times, then returned to the other members of his group who were in a tall tree of *Anogeissus leiocarpa* (Combretaceae) in the area where the fight erupted. The SE pair quickly fled toward the south, leaping from tree to tree. As quiet slowly resumed, Esaka's group resumed feeding on young leaves of *E. suaveolens*. During the episode, both Esaka and Mouka gave more than 10 loud calls. The SE pair stayed in the southern area until 18:45, feeding on the young leaves of *Lonchocarpus cyanescens* (Leguminosae) and resting from time



Figure 3. The corpse of Celi, a 2-month-old white infant white-thighed colobus who died during an intergroup encounter. Photograph by R. Chabi Ota.

to time until moving to their sleeping site. Mouli carried Celi's corpse for several hours, but she was not seen carrying it at the end of the day. The infant's corpse was found on the forest floor the following morning. No thorough inspection of the corpse was conducted due to the sanctity of the species in this forest. For this reason, sex of the infant remains unknown (Figure 3).

For several days following the incident, Esaka behaved extremely aggressively towards the SE pair (but data were not collected on January 22-23, 2018). During this period, he made several forays into the SE pair's area. Mouli and the SE pair (Mouka and his female) did not appear to suffer from injuries. During the next two and a half months, the two groups' membership remained the same. After the infanticidal episode, we did not observe Mouli mating with any males, although she was often seen sitting close to Esaka.

DISCUSSION

In this study, males were the most aggressive participants during the IGE. This observation is consistent with observations made in *C. guereza* in Kakamega Forest in Kenya (Fashing 2001), *C. vellerosus* at BFMS (Sicotte & Macintosh 2004), *C. polykomos* in Tiwai (Dasilva 1989) and in Tai NP (Korstjens *et al.* 2005), *C. angolensis* in Ituri Forest in the Democratic Republic of Congo (Bocian 1997), and *C. satanas* in Lopé Reserve in Gabon (Fleury 1999). In *C. guereza* in Kakamega, the functions of IGEs tend to be that males directly defend females and also engage in indirect mate defense via food resource defense, although females occasionally defended food sources (Fashing 2001). At BFMS, female *C. vellerosus* participated in only

some aggressive encounters and they were the targets of male aggression in half of the IGEs that occurred in their study groups (Sicotte & Macintosh 2004). For this reason, Sicotte & Macintosh (2004) suggested strong support for the hypothesis that males defend mates via defending food resources. This was corroborated by Teichroeb *et al.* (2012) and Teichroeb and Sicotte (2018). The female resource defense hypothesis was supported in only a minority of cases. In contrast, at Tã National Park, *C. polykomos* females interacted in 74%, and males, in 98% of aggressive IGEs. Females were more often aggressive during the months when the group's diet strongly depended on the seeds of *Pentaclethra macrophylla* (Leguminosae), which is an important hard-to-process food (Korstjens *et al.* 2005). Thus, in this species, female food defense is an important element in intergroup relationships. In the present study, the females of the focal group behaved aggressively even before the adult male of the SE pair attacked the mother of the infanticidal victim. This pattern of aggressive female behavior exhibited by *C. vellerosus* at KSF is similar to what was reported in *C. polykomos* at Tã Forest. At both sites, the contest occurred over an important food source.

The infanticide that occurred at KSF differs from the infanticidal episodes that occurred in the same species at BFMS in Ghana where perpetrators of infanticides were newly immigrated males and the victims were unrelated offspring of resident females of the group. At KSF, the perpetrator of the current case belonged to a different group. Based on the available evidence, we suggest that this particular infanticidal episode that occurred at KSF was a consequence of contest competition over a rare food source (Sussman *et al.* 1994). Mouka's attack on the infant appeared to be a retaliatory response to the NE group's invasion of the feeding site that the SE pair occupied. His behavior appeared to be triggered by the focal group members attempting to monopolize the preferred food source that was located in an area where the two groups' home ranges greatly overlap. Further case studies are needed to examine whether the violent IGE we observed is an exception. At KSF, however, the occurrence of IGEs is rare perhaps because of the large difference in group size and the outcome is often predictable, as large groups tend to win against small groups in primate encounters (Crofoot & Wrangham 2010). Also, it may be rare because the female in the SE pair has no other female to cooperatively defend the group during IGEs over food resources (Korstjens *et al.* 2005).

Although the present study has provided a single infanticidal case during an aggressive IGE,

it underscores the importance of studying primate species at multiple locations to fully appreciate the breadth of behavioral variation in the species.

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