



Aspects of Male Competition in *Colobus vellerosus*: Preliminary Data on Male and Female Loud Calling, and Infant Deaths After a Takeover

Pascale Sicotte · Julie A. Teichroeb · Tania L. Saj

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Abstract Male *Colobus vellerosus* are the main participants in intergroup encounters, and lead incursions in neighboring groups during which they attack infants. Extragroup copulations, all-male groups, and male takeover occur in the species. Here, we provide additional information on behaviors associated with male reproductive competition in *Colobus vellerosus*. We examined 1 resident male loud calling and participation in intergroup encounters in relation to a takeover. We also report a second case of takeover that led to the death of the former resident male and the death of 2 male infants, presumably as a result of aggression from the all-male group. The new resident male wounded the third infant of the group, which apparently died after its mother abandoned it. During the period characterized by the attacks on the infant and after its disappearance, females initiated and participated in loud call bouts with the new resident male. We examine the possible functions of female loud calling, and suggest that in this context, it might force the resident male to call along to indicate his presence.

Keywords black-and-white colobus · female loud call · infanticide · male loud call · male takeover

Introduction

Male reproductive competition can have a profound influence on primate social structure and group membership (Janson 2000). Intergroup male reproductive competition

P. Sicotte (✉) · J. A. Teichroeb · T. L. Saj
Department of Anthropology, University of Calgary, 2500 University Drive N.W., Calgary,
AB T2N 1N4, Canada
e-mail: sicotte@ucalgary.ca

Present address:

T. L. Saj
Department of Anthropology, McGill University, 855 Sherbrooke Street West, Montreal,
Quebec H3A 2T7, Canada

encompasses a wide range of behaviors, from avoidance of other groups and of extragroup males to direct contests through intergroup encounters and male incursions in bisexual units (Cheney 1987; Cords 1987). In species in which females are resident, the contests can lead to male takeover, whereas in species with female dispersal, they can lead to female transfer. Infanticide is also a sexually selected strategy that can result from these contests (Struhsaker and Leland 1987; van Schaik 2000a).

Ursine black-and-white colobus (*Colobus vellerosus*) are folivores that live in uni- and multimale groups (Saj et al. 2005; Wong and Sicotte 2006), with seemingly facultative female transfer (*sensu* Steenbeek 1999a). All-male groups occur in the population (Saj and Sicotte 2005). Males are the main participants in intergroup encounters, and they sometimes lead incursions in neighboring groups during which they occasionally attack infants (Sicotte and MacIntosh 2004), which also occurs in *Colobus guereza* leading to infanticide (Harris and Monfort 2003). The incursions sometimes result in female transfer (Sicotte and MacIntosh 2004). Other manifestations of male reproductive competition in the species include male takeover and extragroup copulations (Saj and Sicotte 2005; Teichroeb et al. 2005). We examine the pattern of male loud calling in relation to a takeover and report on a second case of male takeover, which led to infanticide and during which we heard female roaring in our population for the first time.

Primate male loud calls probably function in male competition by signaling male identity and location to conspecific males and females (Reichard and Sommer 1997; Steenbeek and Assink 1998; Wich et al. 2004). Loud calling is an energetically costly behavior (Wich and Nunn 2002), which in black-and-white colobus involves producing prolonged roars, usually accompanied by vigorous physical displays (Oates 1977; Oates et al. 2000). We examine the roaring behavior of a male *Colobus vellerosus* before and after his group was the target of a successful takeover.

Male infanticide as a sexually selected strategy is most likely to be expressed in species that show some paternity certainty, no birth seasonality, and a lactation period longer than gestation (van Schaik 2000a, b). Though black-and-white colobus share the characteristics, researchers have only recently reported male infanticide in the genus (and only in *Colobus guereza*: suspected cases: Oates 1977; observed cases: Harris and Monfort 2003; Onderdonk 2000). We describe a second male takeover in *Colobus vellerosus* that led to the death of 2 infants; a third disappeared. Male aggression surrounding the takeover also led to the death of the former resident male.

The takeover was associated with female roaring. Female loud calling is rarely reported in the literature outside of duetting gibbons and indris (Leighton 1987; Pollock 1986) and fission-fusion species such as chimpanzees (Clark Arcadi 1996). We provide information on the events surrounding the emissions of roars by female *Colobus vellerosus* and compare them to the contexts in which females loud call in the species and in closely related species: *C. polykomos* and *C. guereza*.

Methods

Study Site and Subjects

Black-and-white colobus are arboreal monkeys, generally restricted to tropical rain forests of Africa, but also living in drier habitats associated with riverine or groundwater

forests (Struhsaker and Leland 1987). Sicotte has supervised collection of data on the population of ursine black-and-white colobus (*Colobus vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) since 2000. BFMS is a small (1.9 km²) dry semideciduous forest in the Brong-Ahafo region of Ghana. The population of black-and-white colobus is increasing and is currently estimated at 217–241 individuals in 15 bisexual groups (Wong and Sicotte 2006). Group sizes ranged from 4 to 38. BFMS is connected to several smaller fragments of forests by a narrow riparian forest; black-and-white colobus are present in some of the fragments, and groups or individuals apparently travel between fragments (Fargey 1992; Saj *et al.* 2005; Wong and Sicotte 2006). The annual diet of *Colobus vellerosus* is dominated by leaves (79% of feeding time: Saj 2005).

Roars

Group B provides the data for the male roaring in relation to the first takeover. The actual takeover and the following social changes, including a series of attacks on an immature, were described by Saj and Sicotte (2005). Before the male takeover, the group consisted of 1 adult male (T), which was the only resident male in the group for ≥ 9 mo before the takeover; 3 adult females; and 4 immatures. After the takeover, the group consisted of the original 7 members, including T plus 7 males that belonged to an all-male band. The males stayed with the group for ≥ 7 mo when Saj left the field.

We have 839 h of observation on B *ad libitum* and focal during which we recorded all occurrences of roaring and intergroup encounters. Roaring bouts had to be separated by ≥ 10 min to be considered distinct. We focus on T's roaring in 3 periods: 1) baseline: August–November 2000, 288 h of observation; 2) pre-invasion: January–April 2001, 147.5 h of observation just before the takeover; and 3) post-invasion: April–August 2001, 403.5 h of observation. During the last period, T sometimes roared with other males of the group. Consistent with previous colobine research (Fashing 2001; Korstjens 2001; Oates 1977; Stanford 1991; Steenbeek 1999b), intergroup encounters occurred when 2 groups were < 50 m from each other. Intergroup encounters and roaring bouts are not temporally associated in *Colobus vellerosus* (Sicotte and MacIntosh 2004).

We compared T's morning call rate, defined as the roars occurring between 0600 and 0700 h; the rate of all his roars; the number of days T roared or not; his response rates to roars emitted by other groups (the roars had to follow immediately the initial roars emitted by other group to qualify as a response); and the rate of intergroup encounters involving group B across periods. We acknowledge that this is a descriptive, preliminary assessment of male roaring ($N=1$ male) in relation to a takeover ($N=1$ takeover) and suggest that one should interpret the results cautiously.

Second Male Takeover, Infanticide, and Female Roars

In June 2003, we began to follow group RT, a small habituated group in which individuals were recognizable ($N=10$; 1 male, 5 females, 1 juvenile female, and 3 male infants *ca.* 3 mo). Soon after, a male takeover occurred. We observed RT for 6 d (41.5 h) between June 22 and July 23, 2003 (before the takeover), and for 13 days (August 8–18 and September 6–8; 93 h) after the takeover. We recontacted

the group in June 2004. We provide data collected after the takeover that relate to male attacks on the remaining infant in the group and on female roaring.

Results

Male Roars in Relation to Takeover

Eighteen percent of T's roars were morning calls. Our sampling effort between 0600 and 0700 h was not equal between periods (24, 8.5, and 10 h, respectively for the 3 periods), but suggested that T emitted fewer morning calls before the invasion. The mean rate is .25 roars/h in the baseline, 0 in the pre-invasion period, and .1 in post-invasion (range 0–1 loud calls [LC]/h).

We also combined all roars, morning and day calls, for full days—days with ≥ 7.5 h of observation: respectively 24, 9, and 33 d for the 3 periods. In the baseline, T roared .05/h (range 0–2 LC/d), whereas the rate in pre-invasion was .01 roars/h (range: 0–1 LC/d) and .03/h in post-invasion (range: 0–2 LC/d, Fig. 1). We also looked at the daily presence vs. absence of roars emitted by T. We grouped the days between baseline and peri-invasion (pre- and post-invasion) because the small number of days in the pre-invasion period meant that expected frequencies were < 5 in $> 20\%$ of the cells. In the baseline, T roared at least once in 11 d out of 25 (.44), vs. 10/42 (.24) in peri-invasion ($\chi^2=5.2$, $N=77$ days, $df=1$, $p<.05$).

T answered 21% of roars from other groups in the baseline (4/19; Fig. 2), whereas his response rate in the pre-invasion period fell to 0 (out of 24 roars heard from other groups). In post-invasion, his response rate rose to 30% (8/27).

Intergroup encounters involving B occurred more often in the pre-invasion period, when the hourly rate was .12 (17 encounters in 147.5 h of observation; Fig. 3) vs. .02 in the baseline period (5 encounters out of 288 h) and .05 in the post-invasion period (19 out of 403.5 h). We can not compare rates of encounters initiated by T in the 3 periods because we have no datum on initiation of intergroup encounters.

Fig. 1 T roaring rate. BL = baseline period; PreI = pre-invasion; PostI = post-invasion.

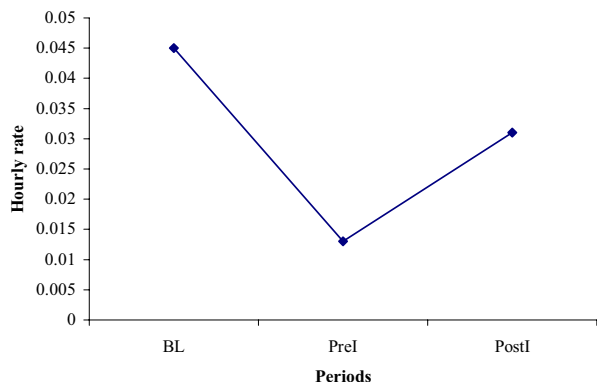
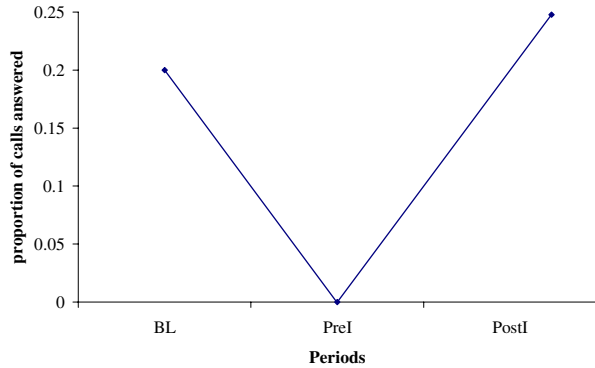


Fig. 2 Proportion of roars from other groups answered by T. BL = baseline period; PreI = pre-invasion; PostI = post-invasion.



Second Male Takeover

Throughout July 2003, Sarah Wong conducted census work in BFMS and surrounding forest fragments. On July 28, she recorded for the first time the presence of an all-male group in RT's range. The males were fighting, and because of the number of males involved, it was not clear if the fight involved the resident male of RT or not. On August 3, Wildlife Division staff found the body of an adult male in the area where the fighting males had been observed (A. Dassah, BFMS Wildlife Officer, *pers. comm.*). It was in an advanced stage of decomposition, and was buried in the monkey cemetery of the sanctuary.

Teichroeb contacted RT on August 8. The resident male and 2 of the 3 infants were missing, and there were a new adult (ST) and subadult male in the group. Teichroeb found the decomposed body of an infant in RT's range on the same day.

Infanticide and Mating Events

During the first day of observation post-takeover and for the following days (August 8, 10, 11, and 12), the new adult male (ST) directed aggression toward female BL's infant at least once and up to 4 times/d (Table I). The aggressive acts ranged from chases to aggression with physical contact. BL and other females intervened on behalf of the infant in several of the aggressions. On August 12, ST injured the infant. On the 13th, BL remained with her infant on the periphery of the group. She

Fig. 3 Rate of intergroup encounters involving group B. BL = baseline period; PreI = pre-invasion; PostI = post-invasion.

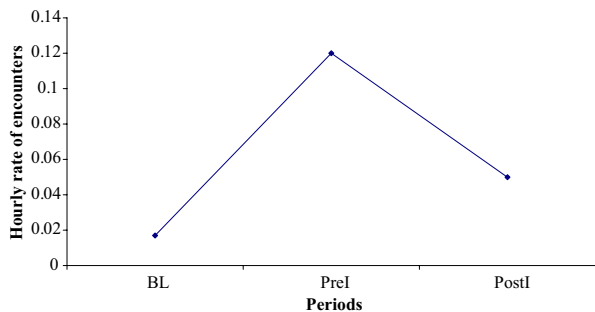


Table I Events surrounding the disappearance of the last infant

Date	Description
Aug. 8	1508: Loud calls (LC) initiated by females, ^a males join in chorus. 1554 and 1654: ST chases BL with her infant, she flees. 1746: Females initiate LC.
Aug. 9	0915: ST flees from a scuffle.
Aug. 10	1013: LC, scuffle. 1224: ST chases the infant. A female chases ST. 1451: Three <i>che</i> sounds but no roaring follows. 1454: ST and a female fall to the ground after a scuffle. She presents and chatters at him. 1455: ST attempts to mount PO (1 of the females without infant at the time of takeover).
Aug. 11	1617: ST chases the infant; mother BL intervenes. Another female intervenes, chatters, and presents to ST. The infant flees, and BL stays between him and ST.
Aug. 12	1051: ST chases and attempts to grab the infant; three females chase him and the subadult male out of the tree. 1444: ST chases and attempts to grab the infant; BL intervenes. 1500: ST chases infant; females initiate LC and ST joins them. 1532: ST chases and injures the infant's leg. Four females, including BL, intervene. 1700: BL still carries the infant.
Aug. 13	0902: BL and the infant sit in a separate tree from the rest of the group. 1218: Females initiate LC, Male ST joins in. 1542: ST rushes toward the injured infant; BL intervenes. 16:01 Scuffle and grunting in the low bushes. BL does not have the infant anymore and stares at the ground. At 1639, 1709, and 1719, females initiate LC; male ST joins in. 1800: BL settles for the night without the infant, away from attack site. She becomes agitated and returns when Teichroeb goes to the attack site to search for the infant but leaves again when Teichroeb leaves.
Aug. 14	0830: BL is between the tree occupied by ST and rest of the group, and the tree where her infant rests. The infant limps and squeals intermittently. 0903: Females initiate LC; ST joins in. 1051: ST approaches the infant; BL intervenes. 1448: The group (with BL) moves away from the infant as they forage. 1800: The group sleeps 60 m from last known location of the infant.
Aug. 15	Infant not seen again
Aug. 16	Infant presumed dead. No female loud calling, no copulation. 1534: LC initiated by females, ST joins in. 1545: ST mounts BL.
Aug. 17	0913: LC initiated by females, ST joins in. 1312: One <i>che</i> sound
Sept. 6	1643: One <i>che</i> sound
Sept. 7	1355: PO grooms ST.

^a *che* sounds preceded all female initiated loud calls.

foraged little, positioning herself between the injured infant and ST. On the 14th, BL left her injured infant high in a tree and foraged low with the rest of the group. We did not see the infant subsequently.

On August 10, ST attempted to mount PO, one of the females that did not have an infant at the time of the takeover. On August 17, ST attempted to mount BL. Teichroeb left the site September 10, 2003, so we could not document further the copulations involving the new male and the females of RT.

Female Roars

After the takeover, when ST regularly targeted the last infant, and after the infant's death, the females of the group initiated and participated in roaring bouts. Female roaring was slightly higher in frequency than male roaring. It started with 1 female emitting a loud *che* sound that was answered by several *che* from other females. One or several females then usually started to roar; on a few occasions, female *che* was not followed by female roaring (Table I). They roared 2 or 3 times, then a female

emitted a *che*, and female roaring started again. Female roaring always prompted ST to begin a roaring bout. When the male roared, females usually roared with him and displayed by jumping on branches (jump about; Oates 1977). The female roaring did not stop entirely after the death of the infant, as we heard it on a few occasions in the last days of observations. During the period after the male takeover, the females also participated in the roaring and the jump displaying with ST during his morning call bouts, though they did not initiate the bouts.

Subsequent Births in the Group

The next year (June 18, 2004), Teichroeb contacted RT and identified the resident male (ST) based on characteristics of his tail and face. RT had 5 new infants (4 black-and-white infants about 2–3 mo old, and 1 white infant 1–2 wk old). The black-and-white infants belonged to the 3 females that lost infants the previous year (BL, FR, and JE) and to PO. The youngest, white infant belonged to TR, which seemed nulliparous the previous year based on her short nipples.

Discussion

The events we described provide intriguing, albeit quantitatively limited, data on events apparently stemming from male intergroup competition in *Colobus vellerosus*. Our preliminary results indicate an inverse relationship between T's roaring and his participation in intergroup encounters. His roaring rate was the lowest immediately before and after the takeover. It was also before the takeover that he answered the least roars from other groups, and that his group was involved the least in intergroup encounters.

Loud calls are energetically costly to produce (Wich and Nunn 2002). It is likely that the frequency at which males call varies between and within individuals, because the calls may advertise male competitive ability (Cowlshaw 1996). Vulnerable males, which are past prime or wounded, may not advertise their location as much as males in their prime do (Steenbeek *et al.* 1999). T may have been vulnerable in his position as the only resident male in the period immediately before the takeover of his group. Whether his vulnerability was internal, i.e., he was aging, or weakened physically or external, i.e., due to the fact that the all-male band was ranging in the area and represented a threat, is not known. Also, it is unknown whether the apparent differences that we report would be perceived by the subjects themselves. Though our data are limited, they are consistent with patterns of roaring in *Presbytis thomasi* (Steenbeek *et al.* 1999).

Nevertheless, we cannot rule out that the trends that we report in roaring rates and in intergroup encounters might be caused by factors other than an increased vulnerability of the resident male. For instance, they may have been due to differences in food availability during different periods of the year, or to differences in our sampling regimen between the baseline period and the peri-invasion period. Alternatively, B and surrounding bisexual units might have been less habituated in 2000—during the baseline—which could have caused more roaring and less intergroup encounters.

A plausible and parsimonious interpretation of the information presented on the second takeover is that the 2 new males in RT were part of the all-male band that attacked the group. Perhaps the males fatally wounded the former resident male. The new adult male regularly attacked the last infant of RT, which apparently died of its wounds, suggesting that the new male(s), with or without other members of the all-male band, may also have been responsible for the death/disappearance of the other 2 infants.

It is also plausible that the new adult male sired the infants that were present in RT in June 2004, and hence that the death of the 3 infants during and after the takeover induced the females to return to estrus. Indeed, assuming that gestation is about 6 mo in *Colobus vellerosus* (195 d in *C. satanas* and 170 d in *C. polykomos*: Harvey et al. 1987; 186 d in *C. polykomos*: Dasilva 1989), and if we are correct in estimating the ages of the black-and-white infants, the 4 infants we observed in June 2004 would have been conceived ≤ 1 or 2 mo after the takeover and the infant deaths. The interbirth interval would therefore be ca. 1 yr, considerably lower than interbirth intervals documented so far in wild black-and-white colobus when the previous infant survived (24 mo, $N=4$; Dasilva 1989).

An intriguing behavior that occurred in association with the takeover was the female roaring and jumping display, which is usually a male behavior in black-and-white colobus (Oates 1977). The female roaring we observed always prompted the male to roar as well. Although we started observations at BFMS in 2000, we had never, before this case, heard females roar. Female loud calling occurs in fission-fusion species such as the chimpanzees (Clark Arcadi 1996), in which it seems to be used mainly for interparty communication. It also occurs in gibbons and indris, in which a male and female engage in duets that probably advertise the fact that the individuals are paired, and the location of the pair in the territory (Leighton 1987; Pollock 1986). When the female calls, the male may be forced to call, because he would otherwise advertise his absence, and possibly open the door to extragroup copulations (Reichard and Sommer 1997). Female songs in gibbons also seem related to territorial defense (Cowlshaw 1992, 1996). Korstjens (2001) reported female roaring during intergroup encounters in *Colobus polykomos*, a species in which females participate in intergroup contest competition. In wild *Colobus guereza*, female roaring apparently occurs in association with intense agonism in the group (Tara Harris pers. comm.).

At BFMS was the female roaring simply caused by the excitement or the aggression surrounding the male takeover? This explanation seems to be insufficient, because we did not hear female roaring during the first takeover, which also involved an all-male band and attacks on an immature (Saj and Sicotte 2005). However, 2 elements differed between the takeovers: the immature survived and the former resident male stayed in the group and eventually protected him from male attacks.

Is it possible that female roaring in *Colobus vellerosus* might be related to resource defense, as it may be the case in *C. polykomos* and in gibbons? This seems unlikely, because female *C. vellerosus* typically do not participate in intergroup encounters (Sicotte and MacIntosh 2004), and females do show no contest competition over food resources, even when higher quality items such as seedpods, fruits, and flowers are available (Saj 2005). Further, we recorded the female roaring in August, when

availability of high-quality items is the lowest and mature leaves are not only widely available but also provide 90% of the diet (Saj 2005).

Could female roaring be a way to induce the male to call? If females in his group start roaring, a male may not have a choice but to roar also because female calls give away the group's location. If the male does not call, it sends out the message that the group is either maleless or that he is vulnerable. Either way, the group would be susceptible to incursions by extragroup males, as suggested for gibbons by Reichard and Sommer (1997). More observations on the context of occurrence of female roaring are necessary before we can reach a more definitive conclusion.

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