BRILL

The vocal repertoire of an African colobine, *Colobus angolensis ruwenzorii*: a multi-level society compared to congeners in stable groups

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Abstract

Vocal behaviour offers a window into understanding the social life and evolution of animals. Colobine monkeys show great interspecific and interpopulation variation in their social organization and behaviour. Recent research has shown that Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) differ substantially from other black-and-white colobus in forming a multi-level society. No previous research has been conducted on the communication of *C. a. ruwenzorii*, but the social complexity hypothesis for communication suggests that more complex societies should evolve more complex communication repertoires. Our objective was to catalogue the vocal repertoire of *C. a. ruwenzorii* at Nabugabo, Uganda, and to compare it with the data available on congeners regarding intergroup tolerance, vocal repertoire size, and acoustic and behavioural features of vocal communication. Vocalizations were subject to spectrographic and behavioural analysis, and a descriptive analysis of each vocalization type was made. The influence of a few environmental and social factors on calling rates was also examined. We describe five vocalizations (i.e., the snort, roar, squeak, scream and pok) and one non-vocal signal (i.e., the tongue click) in this subspecies and their contexts. Distinct alarm calls are made for dogs, and these are given more often near the edge of the forest where humans frequent. We did not find that *C. a. ruwenzorii* showed a greater vocal repertoire than *C. guereza* or *C. polykomos*, which do not live in multi-level societies. Further, preliminary data do not indicate greater calling rates in larger core units of *C. a. ruwenzorii* compared to smaller units. These findings support the view that these primates' vocalizations tend to be relatively conserved despite large differences in social organization.

Keywords

primates, primate communication, vocalizations, spectrographic analyses, social system, social complexity hypothesis, colobines.

Résumé

L'étude de la communication vocale permet de mieux comprendre la vie sociale et l'évolution des animaux. Les singes colobes présentent une grande variation interespèce et interpopulationelle en ce qui a trait à leur organisation sociale et à leur comportement. Des recherches récentes ont démontré que le colobe angolais de Rwenzori (*Colobus angolensis ruwenzorii*) diffère considérablement des autres colobes noirs et blancs, puisqu'il forme une société multi-niveaux. Jusqu'à présent, aucune étude sur la communication de *C. a. ruwenzorii* n'a été conduite, mais l'hypothèse de la complexité sociale en communication animale prédit que les sociétés plus complexes devraient développer des répertoires vocaux plus complexes. L'objectif de cette étude était de cataloguer le répertoire vocal de *C. a. ruwenzorii* à Nabugabo, en Ouganda, et de le comparer aux données disponibles sur ses congénères en ce qui a trait au niveau de tolérance intergroupe, à la taille du répertoire vocal et aux caractéristiques acoustiques du répertoire vocal. Cinq vocalisations (le grognement, le rugissement, le piaulement, le cri et le pok) et un signal non vocal (le cliquètement) ont été entendus lors de cette étude ; chaque signal est décrit dans cet article. *C. a. ruwenzorii* utilise aussi des cris d'alarme distincts en présence de chiens, et ces cris sont donnés plus fréquemment à l'orée de la forêt, un lieu fréquenté par les humains. La présente étude indique que *C. a. ruwenzorii* n'a pas un plus grand répertoire vocal que *C. guereza* ou *C. polykomos*, qui tous deux ne forment pas de sociétés multi-niveaux. De plus, des données préliminaires indiquent que la fréquence de vocalisation n'est pas plus élevée dans les unités centrales qui contiennent un plus grand nombre d'individus. Ces résultats appuient l'idée selon laquelle les vocalisations de ces primates sont relativement similaires (conservées) malgré d'importantes différences au niveau de l'organisation sociale.

Mots clés

primates, communication, vocalisations, analyses spectrographiques, système social, hypothèse de la complexité sociale, colobinés.

Resumen

El estudio de la comunicación vocal permite mejor comprensión de la vida social y la evolución de los animales. El mono colobo demuestra una gran cantidad de variación interespecífica y inter poblacional en lo que se refiere a su organización social y su comportamiento. Investigaciones recientes han demostrado que el mono colobo angoleño de Rwenzori (*Colobus angolensis ruwenzorii*) difiere considerablemente de los otros colobos negros y blancos porque él forma una sociedad de múltiplos niveles. Hasta ahora, ningún estudio se ha concentrado en la comunicación de *C. a. ruwenzorii*, pero la hipótesis del efecto de la complejidad social en la comunicación de animales predice que las sociedades más complejas deberían desarrollar repertorios vocales más complejos. El objetivo de esta investigación era de catalogar el repertorio vocal de *C. a. ruwenzorii* en Nabugabo, en Uganda, para compararlo a los datos disponibles sobre sus congéneres en lo que se refiere al nivel de tolerancia entre grupos diferentes, al tamaño del repertorio vocal, y a las características acústicas del repertorio vocal. Se oyeron cinco tipos diferentes de vocalizaciones (la queja, el rugido, el chillido, el grito y el pok) y una señal sin característica vocal (el tintineo) durante este estudio; y cada señal está descrita en este artículo. *C. a. ruwenzorii* utiliza gritos de alarma distintos en la presencia de perros y estos gritos están utilizados más frecuentemente en el borde del bosque, donde la presencia de humanos es más común. Demostramos que *C. a. ruwenzorii* no tiene un repertorio vocal más largo que *C. guereza* o *C. polykomos*, los cuales no forman sociedades de múltiplos niveles. Además, datos preliminares indican que la intensidad de la vocalización no está más elevada en las unidades centrales que contienen una cantidad mayor de individuos. Estos resultados apoyan la conclusión que las vocalizaciones de estos primates son rel-

ativamente similares (conservadas) a pesar de deferencias importantes al nivel de la organización social.

Palabras clave
primates; comunicación; vocalizaciones; análisis espectrográficos; sistema social; hipótesis del efecto de la complejidad social; colobinos.

1. Introduction

Auditory communication is vital to survival and reproduction in many animal species. Several important influences on the evolution of acoustic signals in animals have been identified, including environmental effects, sexual selection (Wilkins et al., 2013), and social complexity (Freeberg, 2006; Bouchet et al., 2013). As signals travel through the environment, they are affected by an attenuation of their amplitude, temporal and spectral degradation, and background noise such as wind, rain, and insects (Wiley & Richards, 1982). Signallers have evolved various features to improve their communication range and to enhance the locatability of their vocalizations, including an increase of the amplitude (Sinnott et al., 1975), duration (Klump & Maier, 1990), and number of syllables (i.e., units of sound) of their vocalizations (Brumm et al., 2004). The locatability of a call is of particular importance for dispersed animals who live in densely foliated forests (Boinski, 2000) and/or exhibit fission–fusion dynamics. Sexual selection has been shown to impact acoustic signals when these serve as indicators of caller quality (Fischer et al., 2004; Neumann et al., 2010; Wilkins et al., 2013). The social complexity hypothesis for communication (Dunbar, 1998; Pinker, 2003; Freeberg, 2006) has also gained some support. This hypothesis states that the degree of social complexity (i.e., social organization, social structure, group size, etc.) can impact auditory communication with more signals found in more complex or larger social groups (Bouchet et al., 2013). Thus, species that form large (often tiered) aggregations could be expected to have greater vocal repertoires because they face more challenges in coordinating activity among many individuals (Conradt & Roper, 2005; Couzin et al., 2005). For instance, specific moving calls may be used as a form of voting to come to a consensus about movement time and direction (e.g., Stewart & Harcourt, 1994; Bousquet et al., 2011; Walker et al., 2017). In addition, larger groups may have greater calling rates than smaller groups of the same species (e.g., Freeberg, 2000; Payne et al., 2003; McComb & Semple, 2005) because calling may allow larger groups to stay cohesive (Dunbar, 1998).

Colobine monkeys occur in Africa and Asia, and show great interspecific and interpopulation variation in their diets, group sizes, social systems, and degree of sociality (Fashing, 2011; Kirkpatrick, 2011). Within the black-and-white colobus clade in Africa, there are five species groups (i.e., *Colobus angolensis*, *C. guereza*, *C. polykomos*, *C. satanas* and *C. vellerosus*), most broken up into subspecies. *C. angolensis* is typically divided into seven sub-species across its range from Kenya, in eastern Africa, to Angola, in the West (Mittermeier et al., 2013). Observations on black-and-white colobus monkeys across Africa have indicated that the Rwenzori subspecies of Angolan colobus (*Colobus angolensis ruwenzorii*) may be substantially different from other *Colobus* species (Fashing, 2011). *C. a. ruwenzorii* was first observed to be odd in the *Colobus* clade for forming very large groups (~300–500 individuals) (Fimbel et al., 2001; Plumptre et al., 2002; Miller et al., 2018) that fission and fuse frequently at lower altitudes (Teichroeb et al., 2019). However, work at Nabugabo, Uganda, showed that these groups are made up of many core units within which individuals stay cohesive despite the fluidity of the rest of the group (Stead & Teichroeb, 2019). Work on the same subspecies in Rwanda has also shown this type of social organziation (Miller et al., 2020). Thus, *C. a. ruwenzorii* is forming a multi-level society, which has only been previously documented in the colobines in Asia (Kirk-patrick, 2011). The core units of most multi-level societies in primates are uni-male/multi-female (Grueter & Zinner, 2004); however, *C. a. ruwenzorii* differs with about 50% of core units having two or more reproductive adult males. At least three tiers have now been identified in this multi-level soci-ety: the core unit, the clan, and the band (Stead & Teichroeb, 2019). Patterns of proximity and grooming show that this subspecies is cross-bonded (i.e., males and females are bonded); here again, differing from other black-and-white colobus that have been studied, which are female-bonded (Arseneau-Robar et al., 2018).

This research brings up many questions as to why this subspecies of An-golan colobus is so different from closely related black-and-white colobus, including those of its own species group. Vocal behaviour offers a window into understanding the social life and evolution of animals, but no study has yet been conducted on the communication of this subspecies. Thus, the ob-jective of this project was to catalogue the vocal repertoire of *C. a. ruwenzorii* at Nabugabo and compare it to closely related black-and-white colobus that live in small cohesive groups. Even though studies on the communication

of *C. a. ruwenzorii* are non-existent, the vocal repertoire of closely related *C. guereza* is well-known and provides an ideal comparison. Marler (1972) provides the only systematic study of colobus monkey vocalizations. This work inspired Walek (1978), who conducted a similar study of the vocal repertoire of the king colobus (*C. polykomos*). In the last two decades, studies have also been conducted on specific aspects of the vocalizations of these two species (e.g., Harris et al., 2006; Schel et al., 2009; Schel et al., 2010) and the ursine colobus (*C. vellerosus*) (e.g., Sicotte et al., 2007; Teichroeb & Sicotte, 2010), which allows comparisons.

Seven vocalizations plus one non-vocal signal have been recorded in the genus *Colobus*: the snort, the roar, the caw, the squeak, the scream, the purr, the punk, and the tongue click (Marler, 1972; Walek, 1978; Sicotte et al., 2007; Schel et al., 2009, 2010; Teichroeb & Sicotte, 2010; Teichroeb et al., 2012). This paper will first present each type of vocalization recorded during this study and compare and contrast the vocalizations of each species/subspecies. Secondly, this paper will briefly examine the influence of a few environmental and social factors on the rates of some call types.

First, predictions regarding the characteristics of vocalizations were expected. Relative to *C. guereza*, it was expected that in *C. a. ruwenzorii*:

(1) roars would also co-occur with leaping displays;

(2) alarm calls would present similar patterns in that at least two types of alarm calls (i.e., for terrestrial and aerial predators) would be used since this has been observed in other colobus species (Schel et al., 2009, 2010) and is a widespread phenomenon in animals in general (e.g., Greene & Meagher, 1998; Zuberbühler, 2001; Platzen & Magrath, 2005);

(3) squeaks and screams would be similar acoustically and used in similar contexts by individuals with a similar profile (age class and sex).

In terms of the rates of certain call types, we predicted that alarm calls would be more common in areas where dangers were prevalent. In particular:

(4) alarm calls to domestic dogs would be more frequent near the forest edge where humans and their animals occur.

In comparison to *C. a. ruwenzorii*, who form large fluid groups that can reach more than 500 individuals (Fimbel et al., 2001; Plumptre et al., 2002; Miller et al., 2018; Teichroeb et al., 2019), *C. guereza* form small cohesive groups of approximately 10 individuals (e.g., Oates, 1977b; Krüger et

al., 1998; Onderdonk & Chapman, 2000) and are intolerant of conspecific groups (Oates, 1977a). Thus, relative to *C. guereza*, we predicted that in *C. a. ruwenzorii*:

(5) the vocal repertoire would be larger due to the more complex social organization and the difficulties around band coordination;

(6) individuals would call at greater rates, especially when they are in larger core units;

(7) interunit encounters would not be aggressive, and roars would not be used by adult males when units approach to within 50 m (i.e., implying territorial defence; e.g., Fashing, 2001; Korstjens, 2001; Sicotte et al., 2007), since fission–fusion of core units in *C. a. ruwenzorii* shows tolerance.

2. Material and methods

2.1. Study site and species

This study was conducted in and around the Manwa Forest Reserve (0°20′S and 31°52′E) at Nabugabo, in central Uganda. Nabugabo owes its name to Lake Nabugabo, a small lake of 8.2 × 5 km with an elevation of 1136 m, satellite to Lake Victoria (Chapman et al., 2016). Although Nabugabo is surrounded by swamps, the north and west sides include wetlands, grasslands, patches of primary, secondary and degraded forest — including areas with regenerating vegetation —, farmers' fields and buildings (Chapman et al., 2016; Arseneau-Robar et al., 2018; Teichroeb et al., 2019). This study was conducted in one of these patches of mixed primary and secondary forest, an area of approximately 140 ha. Four primate species occur in these forests, including the colobus, vervet monkeys (*Chlorocebus pygerythrus*), thick-tailed galagos (*Otolemur crassicaudatus*), and a few individual red-tailed monkeys (*Cercopithecus ascanius*). Potential predators for the colobus include several species of venomous and constricting snakes (e.g., *Dendroaspis polylepis*, *Dispholidus typus*, *Python sebae*), crowned hawk-eagles (*Stephanoaetus coronatus*) and domestic dogs (*Canis lupus familiaris*) (Adams & Teichroeb, 2020). Dogs are particularly problematic because they roam the forest in packs and have been seen to kill vervet monkeys (Chapman et al., 2016) and colobus traveling on the ground (E. Mujjuzi, pers. comm.).

One large multi-male/multi-female band (TR) was studied. This band has been followed 6–18 days per month, most months, since 2015. It is composed of 12 core units and numbered 132 individuals as of September 2018. Five core units were uni-male/multi-female and seven were multi-male/multi-female (mean size: 11), and all individuals were recognizable by their natural features. Males and females are easy to discern by their genital ring that is 'connected' in males and 'broken' in females. In males, this area is advertised by the presence of large white patch and the hair grows long towards the centre of the patch, forming a white line between the underside of the scrotum and the anus (Teichroeb et al., 2020).

Core units within the band show fission–fusion patterns with one another so group composition varies. All core units were observed throughout the band's home range with no apparent preferential use of certain areas by certain units. Preferential associations are seen among some core units within the band, and this tier of social organization is referred to as the clan (Stead & Teichroeb, 2019).

2.2. Data collection

Data was collected by SPP with the help of Kakeeto Hannington and Mujjuzi Edward, two Ugandan field assistants, from 17 June to 6 September 2018. Five days per week (60 days in total), TR band was followed from 0800 to 1600, for a total of 389 contact hours. One core unit was followed per day. Observers systematically moved through all 12 core units in the band throughout the three-month data collection period as much as possible before starting again with the first one sampled. Each of the 12 core units was thus followed four to five days in total.

2.2.1. Cataloguing the vocal repertoire of C. a. ruwenzorii

Behaviour was recorded via instantaneous scan sampling at 15-min intervals (i.e., the frequency method; Struhsaker, 1975). To ensure that the same individual was not sampled on successive scans, we sampled the most visible individual, followed by the four individuals to their right; then, for the following scan, we chose a different individual and sampled the four individuals to their left, alternating left/right between scans. For each sample, we recorded the time, individual ID (age class, sex), activity (i.e., moving, resting, feeding, grooming, playing), and position of the group (within 50 m of the edge of the forest or not). When measuring the position of the group,

an edge was considered as an area next to roads, farms, or buildings, including areas situated between forest patches. These areas are generally used by humans, often accompanied by their cattle and/or dogs. Measuring this variable allowed us to take into consideration the impact of anthropic factors on the behaviour (including vocal communication) of *C. a. ruwenzorii*. Scans were suspended whenever a vocalization had to be recorded.

All occurrence sampling (Altmann, 1974) was used to record the vocalizations of *C. a. ruwenzorii*. For each occurrence, we kept track of the time, individual ID (age class, sex), type of vocalization, subject distance from the microphone (m), nearest neighbour ID, number of individuals within 5 m, type of contact between the observer and the focal (was the individual seen or only heard), sounds in the background, number of subjects vocalizing, and position of the group (within 50 m of the edge of the forest or not).

Furthermore, to accurately assess roar calling rates and the relationship to core unit size and composition, during nine days, towards the end of the data collection period (24 August to 6 September, 0915 to 1600), we carefully recorded all occurrences of roaring made by the focal unit that day. Roars were chosen for this analysis because they are the loudest and most obvious call type and allowed us to record accurately when calling was coming from the focal core unit, and not from units in close association with the focal unit. Following Oates & Trocco (1983), a one-minute criterion was used in counting roar bouts. A bout was thus considered as several roaring sequences separated from other roaring sequence by a non-roaring period of at least 1 minute. The number of individuals within a specific core unit was used as the 'group size' for this analysis.

2.2.2. Material

Recordings of vocalizations were taken with a Sony PCM-D100 digital recorder and a Sennheiser shotgun microphone (a K6 power module with a ME67 recording head and a MZW-67 foam windscreen). The Sony PCM-D100 digital recorder has an internal flash memory and stores sound in an uncompressed format (WAV). This device has a buffer ('pre-record'), which allows for continuously recording five seconds that will only be saved after having pressed 'record'. Since it is often hard to predict when an animal will start to vocalize, the presence of a buffer avoids the loss of the beginning of a vocalization or the need to continuously record (Fischer et al., 2013). The ME67 recording head is ideal for recording low-pitched vocalizations over longer distances (Fischer et al., 2013). On average, the recordist was 10 to

50 m from the subject. We have no information suggesting that this affected our results.

2.3. *Data analysis*

Vocalizations were subject to spectrographic analysis using Raven Pro 1.5 software (Cornell Lab of Ornithology, 2017) and a descriptive analysis of each vocalization type was made. The structure of each signal was examined, and particular attention was paid to the general energy distribution, the maximum frequency, the duration of the vocalization, the number of syllables, and the presence of peaks and sequences (repetitions). In addition, the behaviour of the individual who was vocalizing and the association in time between vocalizations (e.g., a squeak and a roar) were analysed. This allowed for a comparison with the data previously collected on the vocalizations of the guereza (Marler, 1972), and to a lesser extent, of the king colobus (Walek, 1978). A total of 1133 vocalizations were analysed to determine the calling context and the profile of the individual calling. From these vocalizations, 443 vocalizations were chosen to be examined with spectrographic analysis. Vocalizations that were not analysed with spectrographic analyses were excluded due to a high level of background noise or the fact that multiple vocalizations were occurring simultaneously. Audio files of each vocalization type described below are provided at 10.6084/m9.figshare.12366599.

Additionally, we compared frequency of dog alarm calls that were heard when the monkeys were near the forest edge vs. when they were in the interior of the forest using McNemar's test. We used VassarStats: Statistical Computation Web Site (Lowry, 2018) for this analysis and considered a *p*-value of 0.05 or lower as significant.

3. Results and discussion

3.1. *Vocal repertoire*

3.1.1. *The snort*

Marler (1972) describes snorts as explosive non-tonal vocalizations that start abruptly with a frequency of 1000 Hz and with some portions that can reach 4000 Hz. The snorts of *C. polykomos* have a slightly higher frequency, with a dominant energy that falls between 2500 and 3700 Hz (Walek, 1978). Snorts sometimes sound more like a bark or adopt the form of a train of pulses (Marler, 1972; Walek, 1978). Snorts in *C. a. ruwenzorii* are an explosive
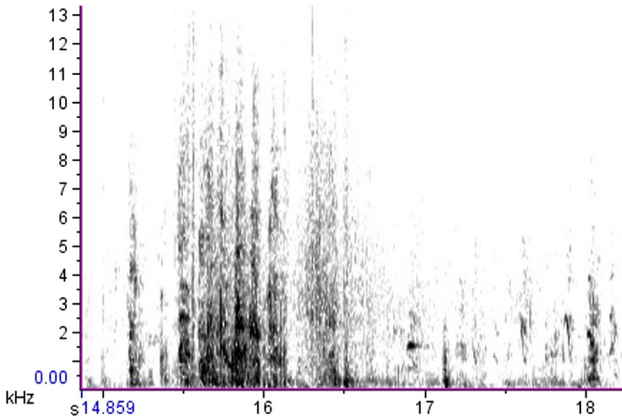
Figure 1. Spectrogram of a snort in *C. a. ruwenzorii*.

sound, but their frequency is not as high. The frequency of snorts varies between 700 and 2850 Hz ($N = 75$) and is generally around 1500 Hz (see Figure 1). Snorts are sometimes followed by roars, and some vocalizations may start as a snort and end as a roar. Snorts may adopt the form of a roar on the spectrogram, which indicates that the distinction between snorts and roars is not always clear. In contrast with *C. guereza* and *C. polykomos* (Marler, 1972; Walek, 1978), snorts in *C. a. ruwenzorii* are not only used by adult males and adult females; they are also used by subadult males and might also be used by juvenile males.

The use of snorts in response to potential predators (dogs or Bateleur eagles [*Terathopious ecaudatus*]) has been reported in the guereza and in the king colobus (Marler, 1972; Walek, 1978). The calling individuals in these species usually approach and glare at the intruder or bounce violently from branch to branch. Snorts may also lead to the approach and inspection of other group members up in the canopy or the escape of group members lower in the canopy (Marler, 1972; Walek, 1978). Therefore, snorts are reminiscent of an alarm call, and it is possible that a truncate form of the snort has this function (Marler, 1972). Snorts can also be part of a roar sequence (later defined), in the case of roars given as alarm calls for example or roars given alone (Marler, 1972; Walek, 1978). Interestingly, this is not the case in *C. a. ruwenzorii*, in which snorts are usually given alone ($N = 71$, i.e., in 94.67% of the cases). In this subspecies, snorts are mainly used during agonistic interactions, when an individual is chasing another individual or is being

chased, or when a female tries to handle the infant of another female. In addition, snorts may co-occur with jump displays and, on a few occasions, these were seen to be used in mating contexts (including the same-sex mating context).

3.1.2. The roar

Roars are the most studied vocalization of the genus *Colobus*. Roars in *C. a. ruwenzorii* adopt a similar structure as in the guereza (Marler, 1972). They are a deep and guttural pulsed sound reminiscent of a noisemaker, composed of a phrase (i.e., several compound pulses that produce a continuous tracing on the spectrogram [Oates & Trocco, 1983]) of several syllables. These phrases are sometimes grouped into a roaring sequence, i.e., when one or more phrases are separated from other phrases by a time space shorter than the duration of any phrase (Oates & Trocco, 1983). Lastly, a series of roaring sequences produced by one individual and with short breaks between each sequence is called a bout, following Oates & Trocco (1983).

Roaring phrases in *C. a. ruwenzorii* generally have between 12 and 15 syllables and last 0.2 to 0.3 seconds. Similarly, roaring phrases of the guereza generally have 15 syllables, but last longer, i.e., 0.7 seconds (Marler, 1972). Roaring sequences in *C. a. ruwenzorii* consist of 1 to 28 phrases that lasts 0.15 to 10.3 seconds (on average they contain 9 phrases and last around 3 seconds, $N = 229$). In both monkeys, each phrase is grouped into two frequency bands. These frequency bands vary between 500 and 1150 Hz in *C. a. ruwenzorii*, but usually between 600 and 700 Hz (see Figure 2), and between 600 and 1200 Hz in the guereza (Marler, 1972). Roars are the loudest vocalization of these monkeys and the vocalization that is most frequently heard (if squeaks are excluded). Marler (1972) notes that the roars of the guereza can be heard up to 1 mi away, which is definitely not the case for the Rwenzori Angolan colobus: roars have been heard up to 0.06 mi away, but never more. Another major difference between the roars of *C. a. ruwenzorii* and the guereza is the presence of explosive snorts of 1000 to 1500 Hz that often precede the first phrase of a sequence in the guereza (Marler, 1972). This has been found in *C. a. ruwenzorii*, but far less frequently ($N = 3$, i.e., only in 1.31% of the cases).

Roars have different intensities. Marler (1972) notes that in the guereza, a low-intensity roar usually consists of a single phrase and a more intense roar consists of four phrases that are generally grouped together into a sequence. The second phrase is usually the loudest and the final phrase is
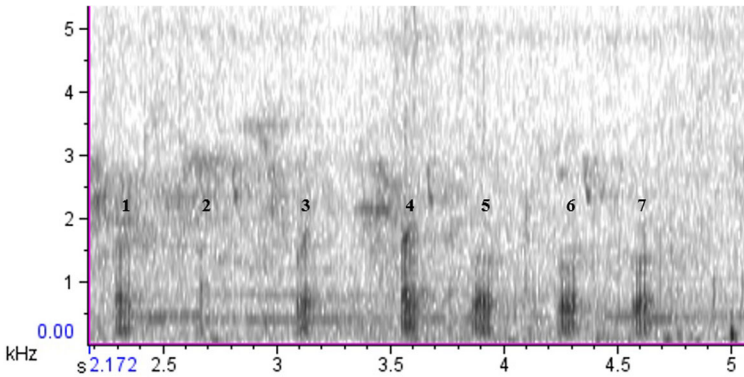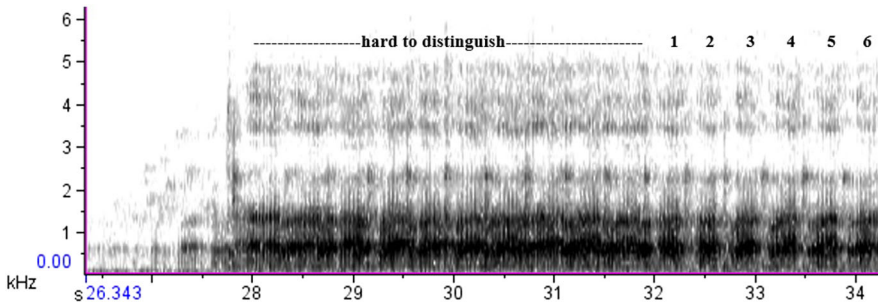
Figure 2. Spectrogram of a roar in *C. a. ruwenzorii*, seven roar phrases.

deeper pitched. This is not really the case in *C. a. ruwenzorii*. Roars some-
times consist of a bout of three to four sequences, but this does not occur
often, and these roars are definitely not the most intense roars. Intense roars
in *C. a. ruwenzorii* generally consist of a unique sequence of 15 to 20 phrases
with a 0.05 to 0.2 second interval between each phrase. Less intense roars
consist of a sequence of fewer than 10 phrases with a 0.2 to 0.3 second inter-
val between each phrase. In the latter, phrases are easier to distinguish, and
one gets the anthropomorphic impression that the monkey is putting more
emphasis on the pronunciation of each 'rrr'.

Intense roars are used as a form of display in both the guereza and the
Rwenzori Angolan colobus. In the most intense displays of the guereza, up
to 20 phrases can be grouped together in a sequence and given consecutively
with a 0.2-second interval between them. Multiple long sequences can follow
each other, and the same individual can roar for up to 20 minutes (Marler,
1972). This has not been observed in *C. a. ruwenzorii*, with individuals
usually not roaring for more than 10 seconds, except in the case of alarm
calls. This can be explained by the fact that individuals often relay one
another in *C. a. ruwenzorii*, but never in the guereza. A few low abbreviated
roars that generally contain only one phrase have also been heard in *C.
a. ruwenzorii*. Bocian (1997) notes that these are usually used in Angolan
colobus of the Okapi Wildlife Reserve, Democratic Republic of Congo (*C. a.
cottoni*), during low-intensity agonistic interactions between males during
both intra and intergroup interactions.

Although roars are given at any time of the day including sometimes at
night, roars are almost always (but not only) given in the early morning,

Figure 3. Spectrogram of a roar chorus in *C. a. ruwenzorii*.

between 0600 and 0700 in the case of *C. a. ruwenzorii*, as a chorus that spreads through the forest from group to group (see Figure 3) (Marler, 1972; Oates, 1977b). Roars are long-range signals used in intergroup communication. They are generally produced by a male situated within his own range, while still at the sleeping site, as a response to the roar of a neighbouring male (Marler, 1972). The number of individuals from the same group who participate in a roar sequence depends on the colobus species: in the guereza, even if more than one male is present, only one male per group will roar (Marler, 1972), whereas in the ursine colobus, all adult males generally roar in synchrony (Teichroeb & Sicotte, 2010). Nonetheless, some individuals roar more than others (more roars per bout, more bouts of roaring) and participate more in roar episodes (Teichroeb & Sicotte, 2010). Depending on the composition of the core unit (uni-male/multi-female or multi-male/multi-female), between one and four adult males participate in roar choruses in *C. a. ruwenzorii*, but all adult males of a core unit do not necessarily roar. Bocian (1997) obtained similar results for the Angolan colobus of the Okapi Wildlife Reserve and notes that roars and jump displays involve at least four adult males.

It could be argued that roars are a way to mark a group's territory or home range (Raemaekers et al., 1984; Mitani, 1987; Catchpole & Slater, 2008) and to advertise the occupation of a sleeping or feeding site (Marler, 1972; Groves, 1973). Since guerezas often engage in intergroup aggression when population density is high (von Hippel, 1996; Fashing, 2001), roars could be sexually selected signals used to assess the quality of other males from afar (Harris et al., 2006). In *C. vellerosus*, roars are used as an agonistic display during intra and intergroup competition between males, and the number of roars a male can produce in sequence is related to his rank (Teichroeb

& Sicotte, 2010; Teichroeb et al., 2012). Roars are energetically costly to produce and advertise the fighting abilities of a male (Wich & Nunn, 2002; Teichroeb & Sicotte, 2010). However, since roars are not often given during close range intergroup encounters, roars could play a role in group spacing, but not in territorial defence. In guerezas, individuals close to the sound may approach and investigate, or withdraw and give squeaks and screams (Marler, 1972). In *C. a. ruwenzorii*, roars are often accompanied by jump displays and even by infant displays. On several occasions, adult males who were handling an infant (on their belly) started to roar and jump display while carrying the infant. These roars are generally accompanied by the squeak of the infant. We even observed a case in which two adult males from two different groups were both carrying an infant and jump displaying in what seemed to be a display toward each other. The handling of infants in roaring displays is not seen in ursine colobus (although infants do follow males and squeak as the male roars and jumps [JAT, pers. obs.]) or reported in other black-and-white colobus, and it should be noted that the degree of infant handling by males appears to be very high in *C. a. ruwenzorii* relative to other colobus monkeys (Stead, unpubl. data).

Furthermore, roars are sometimes given as a reaction to a disturbance in the environment (e.g., a branch breaking, the call of another animal, the presence of a predator), which suggests that roars are a form of aggression or a threat. In these circumstances, the male jumps from branch to branch, slaps the branches while moving, and glares at the intruder (i.e., the leaping display) (Marler, 1972; Teichroeb & Sicotte, 2010). The jumping movements of the colobus are accentuated by the colour of their pelage (black and white) and their trailing tail (white-tipped) (Walek, 1978). Other interpretations of the leaping display suggest that this behaviour is a way to alert the group of a danger or to indicate the direction of group movement (Walek, 1978).

Roars are also used during interspecific encounters (Bocian, 1997). Rwenzori Angolan colobus at Nabugabo live in proximity to groups of vervet monkeys and to solitary red-tailed monkeys. These three monkey species sometimes call at the same time ($N = 2$). The calls are usually initiated by vervets and some colobus answer these calls through roar choruses. The calls of vervets and colobus are very loud in these circumstances; in contrast, red-tailed monkeys produce a short vocalization that sounds like a tongue click and that is barely audible.

Although roars are mostly used by adult males (Marler, 1972; Walek, 1978), roars have also been reported punctually in subadult and adult females and were heard during this fieldwork on *C. a. ruwenzorii*. In ursine colobus, roars by females were heard after a male takeover. Roar bouts generally started with a female producing a loud 'che' sound that was followed by multiple females producing many 'che', and then by one or multiple females roaring twice or thrice. A female then produced another 'che' and other females started to roar again (Sicotte et al., 2007). Female roars were always followed by roars from the new, infanticidal male, which was then followed by females roaring with the male and exhibiting a leaping display (Sicotte et al., 2007). The 'che' described here might be what we classified as a 'snort' (described in Section 3.1.1) since it preceded a roar. Female roaring has also been reported in *C. polykomos* during intergroup contest competition (Korstjens, 2001). The context of occurrence of female roars in *C. a. ruwenzorii* is hard to define, but roars seem to be used during agonistic interactions involving another female or a human observer. On one occasion, an adult female climbed down a branch (she was close to the observers), quickly took a couple of leaves, and then climbed up the branch quickly again while roaring a little. Female roars were also observed in infant handling, mating, and feeding contexts, and before individual movements. No case of females participating in a roar chorus was observed during this fieldwork.

Other studies looked more deeply at the idea that roars could be a form of alarm call. Two types of alarm calls have been found in the guereza and in the king colobus: leopard (*Panthera pardus*) and crowned eagle calls. The leopard alarm call consists of a snort followed by a few roaring phrases. The eagle alarm call consists of multiple roaring phrases that are not preceded by any snort. Both colobus species respond quickly to these alarm calls, and the presence or absence of a snort and the number of roaring phrases seem to be a way to encode the predator type (Schel et al., 2009). Studies of the guereza have shown that these two predators also elicit different behavioural responses. A leopard growl or a leopard call causes the monkeys to scan the area below them, whereas an eagle shriek or an eagle call causes the monkeys to scan the area above them (Schel et al., 2010).

At Nabugabo, *C. a. ruwenzorii* are not preyed upon by felids, which are extirpated; they are mostly preyed upon by dogs, and we suspect that they are also preyed upon by raptors and snakes. One type of alarm call was clearly observed during this fieldwork: the dog alarm call ($N = 47$) (see Figure 4).
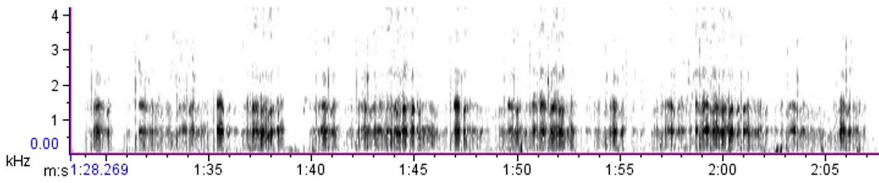
Figure 4. Spectrogram of a dog alarm call in *C. a. ruwenzorii* (at least two groups are calling), including the presence of snorts.

Dog alarm calls have a similar structure to the leopard call described by Schel et al. (2009). They are sometimes preceded by a few snorts and mainly consist of several two-phrases roars ('rrr-rrr'). Just like roar choruses, dog alarm calls are usually given by many individuals at the same time and individuals relay one another. Alarm calls spread through the forest from core unit to core unit, and up to four core units have been heard calling at the same time. Alarm calls can be given for up to 7 minutes and are given by both males and females. Some individuals move and look in the direction of the call, but we also saw some units not calling at all and resting despite the fact that dogs were just beneath them and that other units nearby were calling. Interestingly, the 'typical' two-phrase roar sometimes becomes a louder roar with several phrases (i.e., roars usually used in context where predators are absent), and some dog alarm calls sometimes sound like a mix of alarm calls and roar choruses.

Two olive baboons (*Papio anubis*), a species not typically present at Nabugabo, were seen in the Manwa Forest Reserve during the 2018 field season, and we strongly suspect that *C. a. ruwenzorii* gave a dog alarm call in reaction to their presence: baboon footprints were found next to the trees from which four units were calling. This suggests that what we tend to name 'leopard call' or 'dog call' might be instead a broader alarm call used for large terrestrial mammals. In addition, two cases were observed in *C. a. ruwenzorii* in which an individual vocalized after a large bird (potentially a raptor) came close to them. These vocalizations that might be alarm calls were brief and did not sound like roars, indicating the presence of a potential alarm call used for aerial predators only.

3.1.3. The caw, the squeak, and the scream

Marler (1972) and Walek (1978) establish a distinction between caws on one side, and squeaks and screams on the other side. These vocalizations are all used by infants, juveniles, and adult females. According to the authors,

caws in the guereza and the king colobus consist of a rapid train of pulses with a dominant frequency of 1000 Hz. The pulses can be very short and contain only five pulses, or much longer and contain more than one hundred pulses. Adult females usually give sequences of 5 to 20 pulses (Marler, 1972; Walek, 1978). Caws are used in situations of mild distress, stress, or excitement. For example, caws are given by infants who have been left alone by their mothers, or during weaning, when an infant tries to suckle. Adult females sometimes use caws as a form of defensive threat during aggressive encounters with adult males (Marler, 1972; Walek, 1978). Caws are often associated in time with squeaks and screams. A vocalization can start as a caw and grade into a squeak or a scream in a continuous sequence. Alternatively, a caw frequently takes place between two screams or at the end of a scream (Marler, 1972; Walek, 1978). Although caws seem restricted to intragroup interactions in *C. guereza* (Marler, 1972), they are given at the appearance of neighbouring colobus groups or Sykes' monkeys (*Cercopithecus albogularis*) in *C. polykomos* (Walek, 1978).

On the other hand, Marler (1972) and Walek (1978) present squeaks and screams as loud sounds with higher frequencies. Squeaks last usually 0.1 seconds and have a frequency that rises between 1000 and 2000 Hz and then falls. Multiple squeaks usually occur one after the other in a continuous tone of changing frequencies. Squeaks can grade into longer sounds that last 0.33 to 0.5 seconds and are sometimes drawn into long screams of 0.5 to 1.4 seconds. The tone can be relatively pure or harsh (Marler, 1972; Walek, 1978). Squeaks and screams occur in situations of strong distress such as when an adult female is chased by an adult male, or in reaction to a noisy disturbance in infants (e.g., a leaping display). Squeaks and screams can be used by an infant who is left behind or who tries to suckle during weaning (Marler, 1972; Walek, 1978).

The distinction between caws, and squeaks and screams is not really clear in *C. a. ruwenzorii*, and it seems that the caws defined by Marler (1972) and Walek (1978) are non-existent. It is more appropriate to separate these vocalizations into squeaks and screams in *C. a. ruwenzorii*. Squeaks are almost always given by infants, but can also be given by juveniles, subadults, and adult females. Multiple squeaks usually occur one after the other, with frequencies that range from 600 (in very rare occasions) to 5000 Hz, but that usually range from 2000 to 4000 Hz ($n = 169$) (see Figure 5 and Figure 6). Squeaks definitely have a higher frequency in *C. a. ruwenzorii* than in *C.*
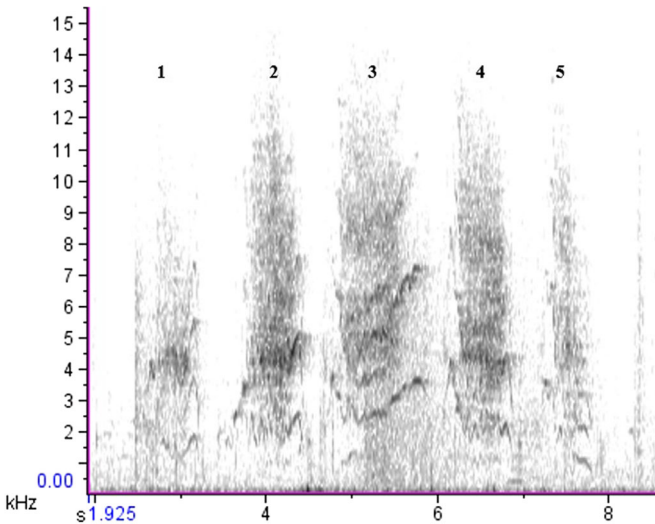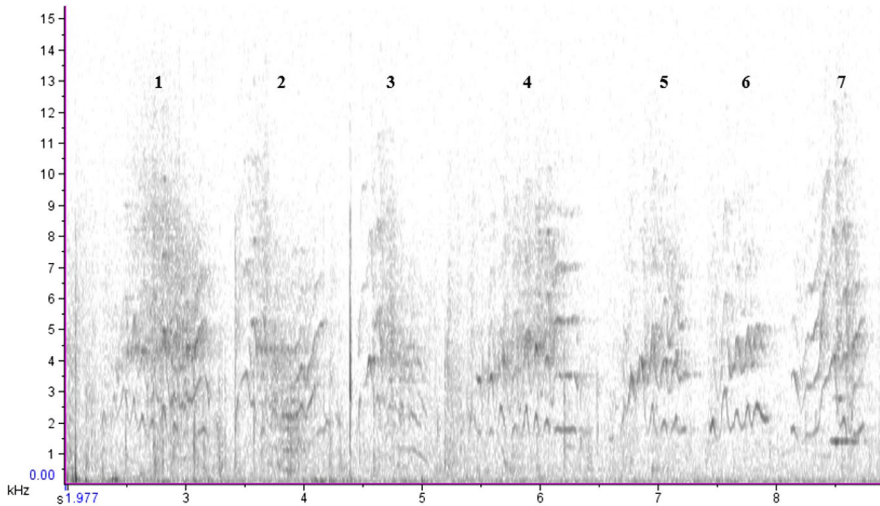
Figure 5. Spectrogram of a squeak in *C. a. ruwenzorii*, at least five peaks (black-and-white infant).

guereza and *C. polykomos*, and although it could be tempting to group them with screams due to their high frequency, the variation in their frequency and their modulation throughout time distinguish them from screams. Squeaks can have up to 50 peaks and last up to 37 seconds. More typical squeaks have around 8 peaks and last 5 seconds. They can be grouped into two to three series of a few squeaks with few breaks of 1 to 2 seconds between each series.

The squeaks of white infants (i.e., younger infants) seem to be different from the squeaks of black-and-white infants. Only a very small sample of white infant squeaks was recorded ($N = 3$), but our results indicate that the squeaks of white infants fall between 3500 and 3800 Hz, and thus have a higher frequency than the average squeak of older black-and-white infants. In general, squeaks are given in similar contexts as caws in the guereza and the king colobus. Squeaks are also strongly associated with the movements of adult males; adult males can abruptly handle an infant, leap display, or move quickly, which causes branches to shake and infants to squeak.

In *C. a. ruwenzorii*, screams are given by juveniles, subadults, and especially adults of both sexes. Screams are an explosive sound somehow reminiscent of the sound of a furious cat. Their frequency falls between 1000 and 3500 Hz, but is usually around 2000 Hz, and they last around 2.5 sec-

Figure 6. Spectrogram of a squeak in *C. a. ruwenzorii*, seven peaks (black-and-white infant).

onds ($N = 37$) (see Figure 7). Although screams do not have a frequency as high as squeaks, screams can be very loud and surprising because they often start loud and stay loud through time. Screams are not given very often and are usually given during agonistic interactions, during play (although play is rarely observed in this subspecies), when tree branches are moving, or by an individual who is almost falling from a tree.
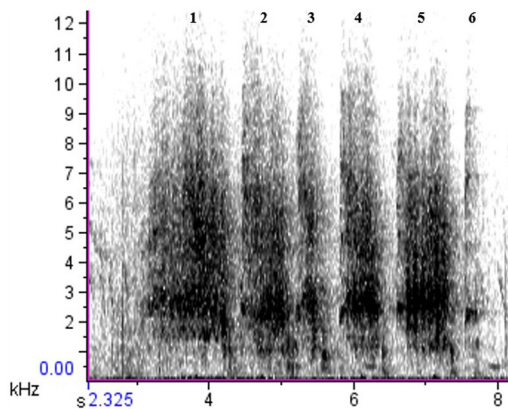
Figure 7. Spectrogram of a scream in *C. a. ruwenzorii*, at least six peaks (adult female).

3.1.4. The purr

Purrs are described as very soft sounds. Few information is available on them since they are rarely heard in *C. guereza* (Marler, 1972) and they seem absent in *C. polykomos* (Walek, 1978). Purrs consist of three or four trains of pulses of about 0.11 seconds each, with a rate of 50 pulses per second. Their frequency varies between 2000 and 2500 Hz (Marler, 1972). These characteristics are based on a very small sample and should not be seen as decisive. It is also possible that purrs are only a variation of the caw (Marler, 1972). Purrs usually occur before group movement and may be used for group coordination in the guereza (Marler, 1972). Purrs were not heard in *C. a. ruwenzorii* during this research. Although the process of group movement and group decision-making is still not understood in this subspecies, individuals tend to urinate and/or defecate before moving (this is the cue that we used throughout the field season). It is therefore possible that a specific behaviour more than a specific vocalization is used by *C. a. ruwenzorii* to initiate group movement.

3.1.5. The punk

Only described in *C. polykomos*, punks are a single-unit phrase produced by infants and adults that last between 0.04 and 0.1 second and is composed of many pulses that rise and decrease in frequency. Their frequency varies between 1300 and 2200 Hz. Although the context of use of punks is unclear, punks could be used as an appeasement or contact call. They are sometimes integrated into an infant's squeaking bout or given by an individual approaching another individual (Walek, 1978). Punks were not heard in *C. a. ruwenzorii*.

3.1.6. The pok

Poks have been heard for the first time during this research and have not been previously mentioned in any colobus monkey. In *C. a. ruwenzorii*, poks are explosive sounds made by adults of both sexes that literally sound like 'pok'. Poks are really quick sounds that last between 0.1 and 1.6 seconds. They are almost always monosyllabic but can be bisyllabic as well. The frequency of poks ranges from 500 to 1600 Hz, and poks can be separated into two categories: low frequency poks, which tend to be more guttural, and high frequency poks ($N = 50$).
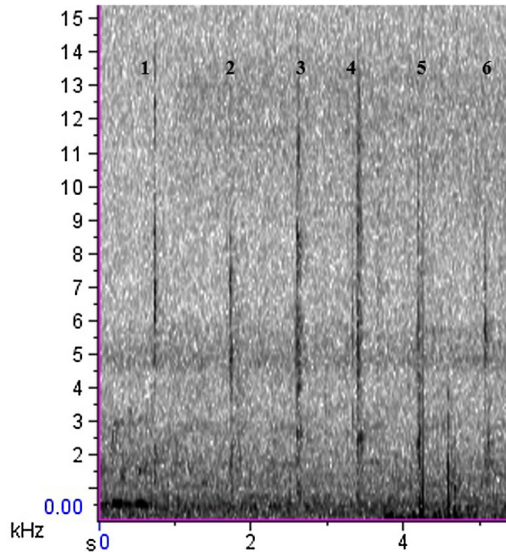
Figure 8. Spectrogram of six tongue clicks in *C. a. ruwenzorii* (adult female).

3.1.7. The tongue click

Tongue clicks are non-vocal sounds that monkeys produce by opening their mouth and clicking their tongue down from the roof of the mouth to the floor. Between one and three clicks are generally produced in *C. guereza* and *C. polykomos*, but it is not rare to hear four or five clicks in a row in *C. a. ruwenzorii* ($N = 48$) (see Figure 8). Tongue clicks are used by both adult males and females but are more frequent among males. Marler (1972) and Walek (1978) note that they are produced by monkeys who are approached by other individuals during intragroup agonistic interactions, and similar patterns have been observed in *C. a. ruwenzorii*. Tongue clicks are also used in intergroup encounters as a form of territorial defence. On several occasions in the guereza, members of two different groups have been observed lining up on both sides of a roadway and tongue clicking while lunging and glaring at each other. Tongue clicks seem to be used as a threat and in attempts to push the opponent to withdraw or show a submissive behaviour. A tongue click can also change into a snort as an individual become more aroused (Marler, 1972).

Soft tongue clicks are also used (Marler, 1972; Walek, 1978). These tongue clicks are not related to agonistic interactions and might be used when an individual is approaching another in a 'friendly' way. These soft tongue

Table 1.

Vocalization/signal type and presence or absence in well-studied *Colobus* species.

Vocalization/signal type	C. guereza (Marler, 1972)	C. polykomos (Walek, 1978)	C. angolensis ruwenzorii (this study)
Snort	Present	Present	Present
Roar	Present	Present	Present
Caw	Present	Present	Absent
Squeak	Present	Present	Present
Scream	Present	Present	Present
Purr	Present	Absent	Absent
Punk	Absent	Present	Absent
Pok	Absent	Absent	Present
Tongue click	Present	Present	Present

clicks also seem to be used to interact peacefully after a fight (Marler, 1972). Tongue clicks that seem to have this function were observed in *C. a. ruwenzorii*, but these tongue clicks did not appear any different (e.g., softer) than regular tongue clicks. We observed cases in which individuals of both sexes tongue clicked when moving closer to another individual, before touching or grooming another individual, before handling an infant or giving an infant to handle to another individual, and when looking in the direction of the observers. In these circumstances, tongue clicking could be a signal of benign intent and have a function similar to grunts in female yellow baboons (*Papio cynocephalus ursinus*) (Cheney et al., 1995) and lip smacks in grooming contexts in chimpanzees (*Pan troglodytes*) (Fedurek et al., 2015). See Table 1 for a summary of the vocal repertoire of *C. guereza*, *C. polykomos*, and *C. a. ruwenzorii*.

3.2. Factors affecting calling rates: some preliminary results

3.2.1. Dog alarm calls and anthropogenic factors

Local people sometimes walk in and around the Manwa Forest Reserve accompanied by their dogs and their cattle, which elicits dog alarm calls. The frequency of dog alarm calls when the focal unit was within 50 m of the edge of the forest (hereafter referred to as 'near an edge') vs. when it was not was used as a proxy to measure the influence of anthropogenic factors on the vocal communication of *C. a. ruwenzorii*. It was found that all dog alarm calls ($N = 31$) were given when the colobus were near an edge. However, considering the fact that *C. a. ruwenzorii* spend more than half their time

near edges (62.01% of their time, $N = 1582$ periods of 15 minutes), we measured the number of alarm calls given when the group was near an edge and divided it by the number of 15-minute periods spent near an edge. We did the same for alarm calls given far from an edge and the number of 15-minute periods spent in these more inner-forest areas. A McNemar's test showed that these two proportions (i.e., 31/981 and 0/601) were significantly different (two-tailed test; $p < 0.0001$) and that individuals produced dog alarm calls significantly more often when they were near a forest edge than when they were not.

3.2.2. *Roars, core unit size, and composition*

Our preliminary descriptive results on roar calling rates did not indicate that these were influenced by the social organization of the core unit (uni-male–multi-female or multi-male–multi-female), the number of individuals in the core unit, the number of adults, or the presence/absence of an edge (see Table 2). This is surprising since large group size is known to affect vocal communication in several animals and since larger groups tend to have greater calling rates (Payne et al., 2003; Conradt & Roper, 2005). Nonetheless, considering our small sample size, these conclusions are far from being definitive and further studies are required. External influences like the presence of dogs or loud, anthropogenic noises can trigger roaring and are difficult to account for in a small sample.

It is also important to highlight the challenges faced when trying to compare the results obtained for *C. a. ruwenzorii* to any other colobus species due to the scarcity of data on this topic and the accepted methods for counting roar bouts. Although Oates & Trocco (1983) indirectly propose a method for counting roar bouts (i.e., using a one-minute interval), they did not apply this method to provide any data in their paper. On the other hand, for *C. a. cottoni*, Bocian (1997) argues that roars given within the same one-hour period may have been elicited by previous roars, especially in cases of 'extended roaring' (i.e., roar periods of 15–20 minutes with breaks between roars; all roars are given by the same individual), and should not be counted as multiple roars. She thus used a one-hour interval when counting roar bouts for the Angolan colobus of the Okapi Wildlife Reserve. A one-hour interval seems arbitrary and long considering the fact that individuals involved in different activities (e.g., feeding context and agonistic context) might call within the same hour and probably not in response to one another. Within a one-hour period, it is also possible that an individual could roar, then the entire group

Table 2.

Roar calling rate, group size, and group composition in nine core units of Rwenzori Angolan colobus.

Focal core unit	Unit composition[1]	No. of individuals	No. of adults	No. of roars/day[2]	Edge (Y/N)[3]
Albizia	UM–MF	6	4	4	Y
Fagara (day 1)	UM–MF	9	5	8	Y
Fagara (day 2)	UM–MF	9	5	13	Y
Polysiasis	UM–MF	9	6	5	Y(1), N(24)
Maesopsis	UM–MF	12	6	7	Y
Lovoa (part 1)[4]	UM–MF	15	7	16	Y(9), N(7)
Phoenix	MM–MF	6	5	13	Y
Lovoa (part 2)[4]	MM	9	7	17	Y
Newtonia	MM–MF	13	10	26	Y(1), N(25)

[1]UM–MF = uni-male/multi-female; MM–MF = multi-male/multi-female; MM = multi-male band.

[2]We followed Oates & Trocco (1983) when counting roar bouts. Nonetheless, Bocian (1997) argues that roars given within the same few minutes might have been elicited by previous roars. She thus uses a one-hour interval when counting roar bouts. Since we were looking at the impact of group size on calling rates, we considered each roar independently and did not control for the fact that individuals might be responding to previous stimuli.

[3]Location of the group when roaring. When roars were made near the edge of the forest vs. the interior of the forest, the number in bracket indicate the number of roars made within each respective position.

[4]The Lovoa core unit split during this period and two subgroups were moving separately. Lovoa (part 2) became an all-male band separate from the Lovoa core unit about a month after data were collected.

could move to another region of the forest, and later, another individual could roar. Once again, it is unlikely that these roars are related to one another. Although Bocian (1997) provides some data on roar frequency — she counted 9 roar bouts in 58 days of observation —, she only considered roars produced by adult males. This is problematic since females in *C. a. ruwenzorii* also roar.

4. Conclusions

This project is the first work ever done on the communication of the Rwenzori Angolan colobus, and the first thorough examination of the vocalizations of an African colobine since the end of the 1970s. The cataloguing of the vocal repertoire of *C. a ruwenzorii* is a vital step that will allow for the ex-

amination of more specific questions related to vocal communication, group movement, and fission–fusion dynamics among core units. While our comparative analysis of the vocalizations of the Rwenzori Angolan colobus, the guereza, and the king colobus allows for a better assessment of the generalities and specificities of the vocalizations of each monkey species, it should be noted that within *C. angolensis*, the Rwenzori subspecies is a social outlier; thus, the vocal behaviour recorded for this subspecies may not be indicative of the whole *C. angolensis* species group.

In terms of the acoustic and behavioural features of the vocal communication of *C. a. ruwenzorii*, it was found that roars usually co-occur with leaping displays, as in the guereza (prediction 1: supported). In addition, the alarm call of *C. a. ruwenzorii* presents similar patterns to the alarm call of *C. guereza*. Roars are used as a form of alarm calls in both of these monkeys and both monkeys have an alarm call for large terrestrial mammals. *C. guereza* also has a distinct alarm call for aerial predators, and although it seems to be the case in *C. a. ruwenzorii*, further studies are needed (prediction 2: supported). It can hardly be concluded that squeaks and screams present similar or dissimilar features. In both *C. a. ruwenzorii* and *C. guereza*, squeaks and screams are given in similar contexts and used by individuals with similar profiles. However, squeaks and screams are different acoustically between these two monkeys: they have a much higher frequency in *C. a. ruwenzorii* and caws seem to be absent (prediction 3: partially supported). In terms of the rate of certain calls, alarm calls to domestic dogs were more frequent near the forest edge (prediction 4: supported).

As previously mentioned, signallers have evolved various features to improve the communication range and to enhance the locatability of their vocalizations. The roars of *C. a. ruwenzorii* are loud enough to be heard by core units nearby (within 0.6 mi), but are not as loud as the roars of the guereza. This could be explained by the fact that roars in *C. a. ruwenzorii* seem to be mainly used for intra-band communication (i.e., they often relay one another) and, to some extent, to ensure unit spacing, but not for territory defence such as in the guereza, where groups are intolerant of conspecific groups. Locatability of the roars and therefore the need to produce loud roars might be more important in the guereza since groups are more dispersed in this species than in *C. a. ruwenzorii*. In addition, since there is evidence that the roars of guereza have been sexually selected to include information on

male body size (Harris et al., 2006), call volume may be an important part of the display.

We did not find support for the social complexity hypothesis for communication (Freeberg, 2006), either in terms of the projections for vocal repertoire size or for calling rates. Despite the fact that *C. a. ruwenzorii* form a multi-level society (Stead & Teichroeb, 2019; Miller et al., 2020), their vocal repertoire does not seem to be larger than the vocal repertoire of the guereza as the social complexity hypothesis would predict. Although poks have only been heard in the Rwenzori Angolan colobus, the vocal repertoire of this primate seems to be smaller than the vocal repertoire of the guereza due to the absence of caws and purrs (prediction 5: not supported). A complication here is that the definition of vocalization types is subjective and some authors tend to present certain primate species as having a broad range of vocalizations while others do not. Di Bitetti & Wheeler (2017), for example, make a distinction between a 'contact note' and an 'aggressive contact note' in the black-horned capuchin (*Cebus* [*Sapajus*] *nigritus*) and Gros-Louis et al. (2008) distinguish between 'peep' and 'intense peep', and 'gargle' and 'intense gargle' in the white-headed capuchin (*Cebus capucinus*). Roaring sequences in *C. a. ruwenzorii* can be short or long, soft or harsh, and are even used as a form of alarm call. Roars could probably be separated into many categories depending on the approach adopted.

Similarly stemming from the social complexity hypothesis, we did not find that individuals in larger core units roar at greater rates (prediction 6: not supported) or that unit composition impacts calling rates. It should be noted that our sample size was small, however. It is also difficult, in a multi-level society, to determine how group size should be defined. In this case, core unit size was used but core units are often in close proximity to one another in *C. a. ruwenzorii*, and although inter-unit encounters may involve some individuals roaring or chasing each other, for the most part, core units show tolerance. They often feed and rest within 50 m of each other for many hours without showing agonistic behaviour (prediction 7: supported). Thus, functionally 'group size' at any one time can fluctuate widely if individuals from different units are included. Further research should count the number of core units in association and compare that with calling rates to determine if larger group size does influence communication. It is noteworthy that Hammerschmidt & Fischer (2019) also found within the baboon clade, which varies widely in terms of social organization and includes stable groups as well as

multi-level societies, that the vocal repertoires of different species contained the same basic call types. These findings and those presented here agree with the idea that without strong selective pressures operating on vocalizations (Wilkins et al., 2013), non-human primates tend to maintain taxon-specific compliments of call types.

This research laid the groundwork for future projects that could explore decision-making and fission–fusion dynamics in *C. a. ruwenzorii*. It has been suggested that within each core unit, a certain individual, the 'broker', might play a greater role in transmitting information to other units and coordinating fission and fusion events, and that all the 'brokers' would be particularly connected to each other (Sueur et al., 2011). This has already been observed in bottlenose dolphins (*Tursiops truncates*) (Lewis et al., 2011) and is worth exploring in *C. a. ruwenzorii*, where decision-making is still poorly understood. Males produce the vast majority of roars that may function in between-unit communication, suggesting that males may act as brokers in this species. There is preliminary evidence ($N = 8$ transfers) that suggests that, although both sexes disperse in *C. a. ruwenzorii* (Arseneau-Robar et al., 2018; Stead & Teichroeb, 2019), females may disperse beyond the band, while males stay within the band. Thus, a higher than average degree of relatedness among the males between *C. a. ruwenzorii* core units may explain their tolerance and provide motivation to share important information via vocalizations. These data provide exciting avenues for future research.

Acknowledgements

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