Vocal Repertoire of Captive Guinea Baboons (Papio papio)

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Abstract: In order to study the evolution of language, it is useful to understand the communicative systems of nonhuman animals. To this end, descriptive ethograms of primate vocal repertoires are the ideal starting point. We examined the vocal repertoire of a group of captive Guinea baboons (*Papio papio*). Twelve vocalizations were readily distinguishable using individual call components and call sequences. Some of these vocalizations were sex and/or age specific (e.g., copulation grunts in females, moans in infants). We compared these vocalizations to those reported in wild Guinea baboons as well as the other baboon taxa. The Guinea baboons share the basic call units with the other baboon species. However, a large degree of variability occurs within call sequences (e.g. number of grunts within a bout, F0 and calling rate [number of grunts/second]). The baboons also showed vocal variability through the combination of different vocalizations (e.g. moans, screams and yaks in varying order and number within a bout) and the use of one vocalization (barks) in a new captive-specific context. The present study complements recent studies on the vocal productions of baboons, and opens several new perspectives on the evolution of language.

Keywords: vocal repertoire, baboons, primate vocalizations, language

1. Introduction

The evolution of speech from more simplistic primate communication may have been a pivotal transition for our species (Smith and Szathmary, 1995;

Snowdon, 2004). However, evidence for how this occurred is scarce, with only a handful of features which define language, such as rudimentary forms of syntax (Ouattara et al., 2009), found in the vocalizations of some primates. It is important to point out, though, that only a small proportion of primate species have had their vocal repertoire described and analyzed (Zuberbühler, 2012). Ethograms are the first step towards better understanding these vocal systems. They can provide the basis for comparative studies, and are especially useful for newcomers to the species and those who work closely with the animals (Fischer and Hammerschmidt, 2002). Careful analysis of vocal repertoires in nonhuman primates also provides the groundwork for systematically tracking the development of more complex vocal systems. Here we present the findings of a study on the vocal repertoire of a group of captive Guinea baboons (*Papio papio*), from which it was possible to determine their ability to produce vowel-like sounds (Boë et al., 2017).

The description of the vocal repertoire of baboons has a complex history due to the wealth of terminology used between and within taxa and researchers, and to indecision regarding species or sub-species status of this primate group. Regarding the latter, the so-called savannah species (Guinea: *P. papio*, Olive: *P. anubis*, Yellow: *P. cynocephalus*, Chacma: *P. ursinus*, Kinda: *P. kindae;* Hayes et al., 1990) have generally been considered to be relatively homologous subspecies with similar vocalizations while the hamadryas baboon (*P. hamadryas*) has been considered, and thus studied, separately as a full species with its own unique vocalizations (e.g., Estes, 1992). Recent genetic evidence suggests that the taxa should be considered as phylogenetic species or biological subspecies. Furthermore, this research has shown that hamadryas baboons have not greatly diverged from the other taxa and share genetic and physical characteristics with Guinea baboons (Newman et al., 2004). Vocalizations are particularly sensitive to the process of speciation (Lanyon, 1969) and their study may serve to provide additional information for baboon systematics. However, while there is a large degree of similarity in the vocalizations between baboon taxa (Maciej et al., 2013a), not all vocalizations seem to occur in all species (Estes, 1992).

The wild studies by Byrne (1981) and Maciej et al. (2013a) comprise the only published reports on the vocal repertoire of Guinea baboons, although notes and some analyzes on individual vocalizations have also been made by Anderson and McGrew (1984), Andrew (1962), Maciej et al. (2013b) and Maestripieri et al. (2005). From these studies, we can determine that vocalizations seem to be important for this species to maintain contact but also to warn off predators (Anderson and McGrew, 1984; Byrne, 1981). However, these studies have limitations. Byrne's ethogram did not include spectrograms or fine-detailed descriptions of all the vocalizations, Maciej et al. (2013a) did not include the vocalizations of juveniles and infants, and a variety of terminology has been used throughout the literature; this can make it difficult to compare the vocalizations or even determine how a particular call sounds.

Analyzes of the vocal repertoires of primates have been conducted by ear (e.g. Byrne, 1981), or using temporal and frequency measures of individual calls and bouts of calls from spectrograms (e.g. Bermejo & Omedes, 1999; Fischer and Hammerschmidt, 2002), and, more recently, cluster and principal component analysis (e.g. Gros-Louis et al., 2008; Maciej et al., 2013a). Using discriminate function analysis, Bezerra et al. (2010) showed that subjective differentiation of vocalizations – that is, by audible and visual inspection – is relatively reliable. Commonly considered structural parameters of vocalizations in these analyzes include duration, frequency range, modulation, harmonics, and noise.

The aim of our study is to identify the full range of vocalizations produced by captive Guinea baboons and provide descriptions of each. After a first presentation of the general principles of our methods, we report below an overview of the different vocalizations in three sections: 'Acoustic description' details the basic features of the vocalization, including variability; 'Context & usage' defines how and when the vocalization was used; the 'Terminology' section lists synonymous vocalizations and their terminology throughout the literature. We then present the results of the formant analyses which were conducted on several categories of vocalizations, including the grunts, barks, wa- (of wahoo), -hoo (of wahoo), yaks, and copulation calls. In our discussion, we will show that such detailed descriptions of the vocal repertoire of a nonhuman primate species open interesting perspectives on the evolution of language. Appendix 1 provides a glossary of the key terms used in this chapter.

2. Methods

This research adhered to the legal requirements of France and to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.1 Subjects and Housing

We recorded the vocal behavior of 31 Guinea baboons (12 males, 19 females, aged between 2 months and 27 years at the start of this study; Appendix 2) which are maintained within three groups at the Rousset-sur-Arc Centre National de la Recherche Scientifique (CNRS) primate center, France (see Fagot et al., 2014 for housing details). This center also houses olive baboons, which are within auditory but not visual range of our subjects.

2.2 Recording of Vocalizations

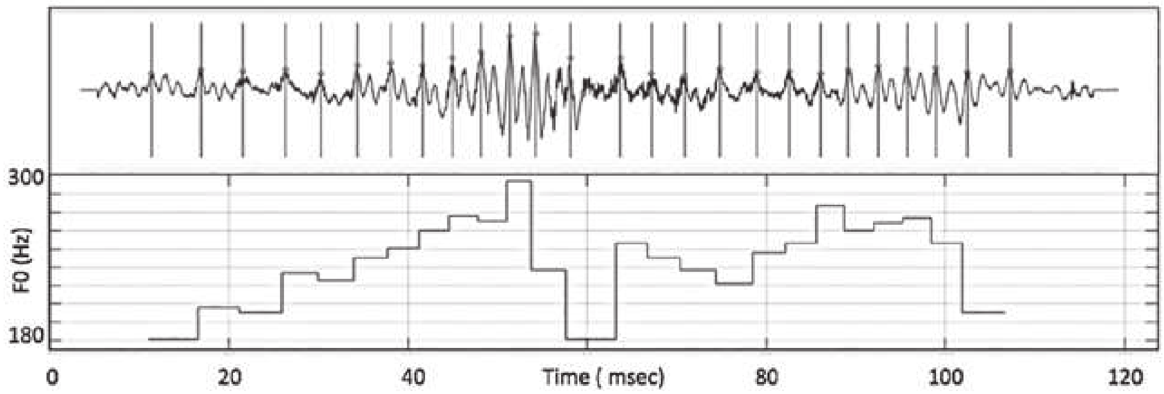
We recorded the vocalizations of the baboons from September 2012 to June 2013, with the behavior, social interactions and context noted. *Ad libitum* opportunistic sampling techniques of spontaneous vocalizations, which included social events and responses to stimuli occurring naturally within their environment (e.g., sheep [*Ovis aries*] passing next to the center), were used to record over 1000 vocalizations. The baboons were accustomed to humans standing and walking by the fence of their enclosures and the presence of the recorders and their equipment did not disturb the baboons from their natural daily activities.

Recording took place between 8:00 and 21:00. We particularly focused on the half hour prior to feeding (16:30–17:00) as the baboons were more vocal, and more consistently vocal, during this time. Recordings did not occur between 17:00 and 18:00 when the baboons were eating, so as to avoid potential distortion of the vocalizations due to chewing and full cheek pouches. Digital Zoom Handy Recorders (H4n) with a Me66 Sennheiser microphone was used to record the vocalizations. This is a super cardioid microphone with a high sensitivity (50mV/Pa ± 2.5dB) and a wide (40Hz – 23kHz) and flat ± 2.5dB frequency response. Recording was conducted at a distance from the baboons from 1m to 20m, with longer distances suitable only for the long-distance vocalizations.

2.3 Vocalization Analysis

After disregarding recordings where the caller could not be identified, or had poor signal to noise ratio, because of disruptive background noise or vocalizations overlapping each other, we created a database of over 1000 vocalizations. Male and female vocal productions were separated in the adult and sub-adult classifications, but were combined for juveniles and infants. This decision was based on the lack of body size differences between male and female juveniles and infants, and the similarity in F0. Vocalizations were then grouped using several methods: by ear, visual inspection using spectrograms, broad descriptive features, and detailed formant analysis. A minimum of 10 recordings per vocalization were analyzed for descriptive features. Our analyses focused on the fundamental frequency (F0), the number of individual call units per vocalization series, the duration of each call or phase, the duration of the interval between two calls in the same bout, the total duration of a calling bout, and formants (F1 and F2). The acoustical analyses of the vocalizations were performed using Praat 6.0.13 for spectrograms and high F0 vocalizations (bark, yak) and (wahoo). A problem using Praat for the measure of F0 is that it relies on the relative periodicity of the speech signal as computed based on short-term autocorrelation. This program is not adapted for inferring F0 for the grunts, barks and chattering, because these calls exhibit some irregularities, additive noise, or very low F0 values (< 60 Hz), i.e. long periods. In our study, F0 was inferred for these latter vocalizations with a home-made Matlab script, which computed F0 from a hand tagging of the periodicity of the acoustic signal (see Figure 1 for an illustration of this procedure).

Figure 1: Illustration of the method used to measure F0 for the grunts, barks and chatterings. The top panel, which shows the auditory signal for a chattering (see the definition of a chattering below), illustrates our hand tagging of the periodicity of the signal. The bottom panel shows the corresponding F0, which was calculated with our Matlab script from the interval durations (bottom panel).



3. Results

3.1 Overview

Twelve distinct vocalizations were distinguishable in the captive Guinea baboons. Some vocalizations were age and sex specific. Table 1 provides the full list of vocalizations and their occurrence per age and sex. Illustrative audio files of each kind of vocalization can be found in the webpage (https://osf.io/nr2ye/) provided as supplementary material. While broad descriptive features of vocalizations were useful in grouping calls and creating distinct categories, formant analysis was only possible in 5 of the 12 vocalizations (grunts, wahoos, barks, yaks, and copulation calls, see below). We selected the clearest recordings for each vocalization per sex/age group for analysis of their broad descriptive features (a minimum of 10 separate recordings was possible).

Table 1: Defining features of each vocalization within the repertoire of Guinea baboons. The calls found within each sex-age category are noted as the percentage recorded, with sample size taken into account. A '-' indicates that this characteristic was not applicable or measurable for that vocalization. ~ indicates that the vocalization was observed in this category but we did not record it. Note that no two vocalizations have the same characteristics.

	Sex-age category							Phases		Number of calls in a vocalisation		Interval duration		F0		Formants			
	Adult males	Adult females	Sub-adult males	Sub-adult females	Juveniles	Infants	Total % recorded	1 phase	2 phases	Single call	Multiple calls	Even	Uneven	< 100	> 100	Present	Absent	Stable	Modulated
Rhythmic grunts	4.97%	2.93%	3.49%	0.52%	1.10%	2.09%	**15.10%**	*			*	*		*		*		*	
Barks	1.18%	5.70%	3.57%	2.09%	3.55%	4.88%	**20.97%**	*		*		–	–		*	*			*
Threat grunts	~	0.26%	0.70%	~	1.05%	0.35%	**2.36%**	*		*		–	–		*	*		*	
Yaks	0.13%	1.83%	0.09%	1.05%	0.64%	3.66%	**7.40%**	*			*	*			*	*			*
Scream	2.09%	2.56%	2.62%	3.14%	4.42%	8.72%	**23.55%**	*		*		–	–		*		*	–	–
Wahoo	6.80%	0.42%	3.57%				**10.79%**		*	*		–	–		*	*		*	
Roargrunts	0.65%						**0.65%**	*			*		*	*		*		*	

	Sex-age category							**Phases**		**Number of calls in a vocalisation**		**Interval duration**		**F0**		**Formants**			
	Adult males	Adult females	Sub-adult males	Sub-adult females	Juveniles	Infants	Total % recorded	1 phase	2 phases	Single call	Multiple calls	Even	Uneven	< 100	> 100	Present	Absent	Stable	Modulated
Male grunts	4.97%		0.26%				**5.23%**	*			*	*		–	–	*		*	
Two-phase grunts	0.39%						**0.39%**		*		*	*		*		*		*	
Copulation call		2.41%		5.23%	0.17%		**1.39%**	*			*		*		*	*		*	
Chattering					0.52%	0.87%	**7.81%**	*			*	*			*	*		*	
Moans						4.36%	**4.36%**	*		*		–	–		*	*		*	
	21.18%	**16.11%**	**14.3%**	**12.03%**	**11.45%**	**24.93%**													

3.2 Vocalizations produced by all or most age and sex categories

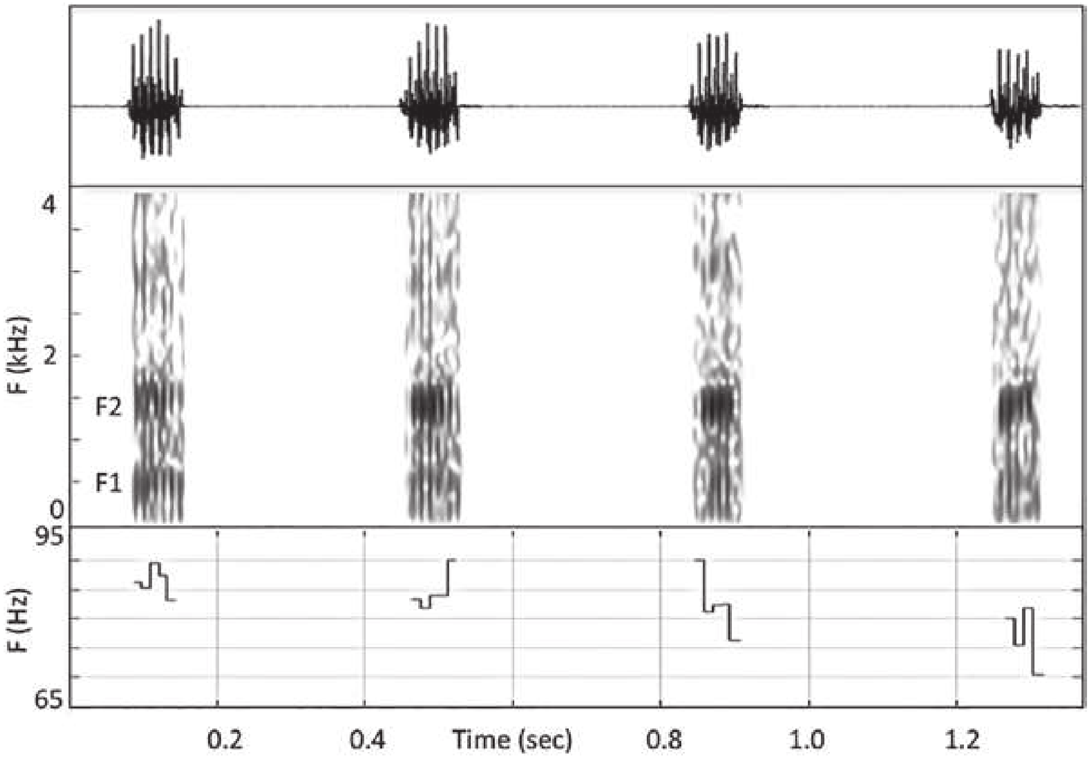
3.2.1 Rhythmic grunts

Acoustic description (see Figure 2): This tonal vocalization is characterized by the presence of multiple, single-phase calls of even temporal spacing, with clear formants (although sometimes only one formant could be detected, particularly when produced by adult males). F0 is low and sometimes changed within a bout but otherwise grunts were acoustically stable in their physical structure within the same bout. Grunt bouts did not vary much between contexts, although faster calling rates were found in contexts 3 and 4 (see below, 'Context & usage'). Calling rates were around 2.2 grunts/s in adults and sub-adults, 1.8 grunts/s in juveniles, and 1.01 grunts/s in infants. Infant grunts showed physical differences from adult and even juvenile grunts, with the loudness and F0 being much higher.

Context & usage: Rhythmic grunts were the most common affiliative vocalizations and were used by all age-sex groups in nine main contexts: 1) towards infants to elicit interaction, 2) towards mothers with infants, 3) after an infant scream, 4) by an individual, not the mother, usually an adult male, holding an infant to its chest, sometimes bouncing it, 5) between hugging adults, 6) by males eliciting a female to copulate, 7) by males after copulation, 8) from dominant animals (or males) to lower ranked females when approaching to groom or sit close by, and 9) by a non-moving group. Grunts were almost always produced as a series of calls (bout). Between 2 and 18 calls per bout were recorded; grunts were considered to belong to the same bout when they were less than 1.5s apart.

The grunts were soft and therefore used only as short distance contact call. The production of grunts by one individual typically did not elicit grunts from other individuals, although this did occur, specifically in contexts 4 and 9. The function of this grunting could not be determined. In this situation, several individuals were sitting within a meter from each other, looking in different directions; they were typically not physically interacting. One individual would begin grunting and the others would then join in. Infants only grunted in response to adult grunts. Grunts were produced with the mouth almost closed, the baboon's ears were twitched backwards and the eyebrows raised with each call.

Figure 2: Rhythmic grunt of an adult female. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants as well as the characteristic vertical lines due to low F0 periodicity (middle panel), and F0 computed with our Matlab scripts (bottom panel).



Terminology: This section lists the terminology used within the baboon taxa literature that, based on descriptions or spectrograms, appears to correspond to the vocalization described here. Grunts (*P. papio*: Byrne, 1981; *P. ursinus*: Cheney and Seyfarth, 2007; Rendall et al., 2005; *P. cynocephalus*: Hall and DeVore, 1965; *P. anubis*: Ey and Fischer, 2011), rapid grunt (*P. papio*: Byrne, 1981), rhythmic grunts (*P. hamadryas*: Ransom, 1981; Smuts, 1985), basic grunt (*P. anubis*: Ransom, 1981; Smuts, 1985), broken grunting (*P. anubis*: Ransom, 1981), low amplitude grunt (*P. ursinus*: Engh et al., 2006), soft grunts (*P. papio*: Anderson and McGrew, 1984).

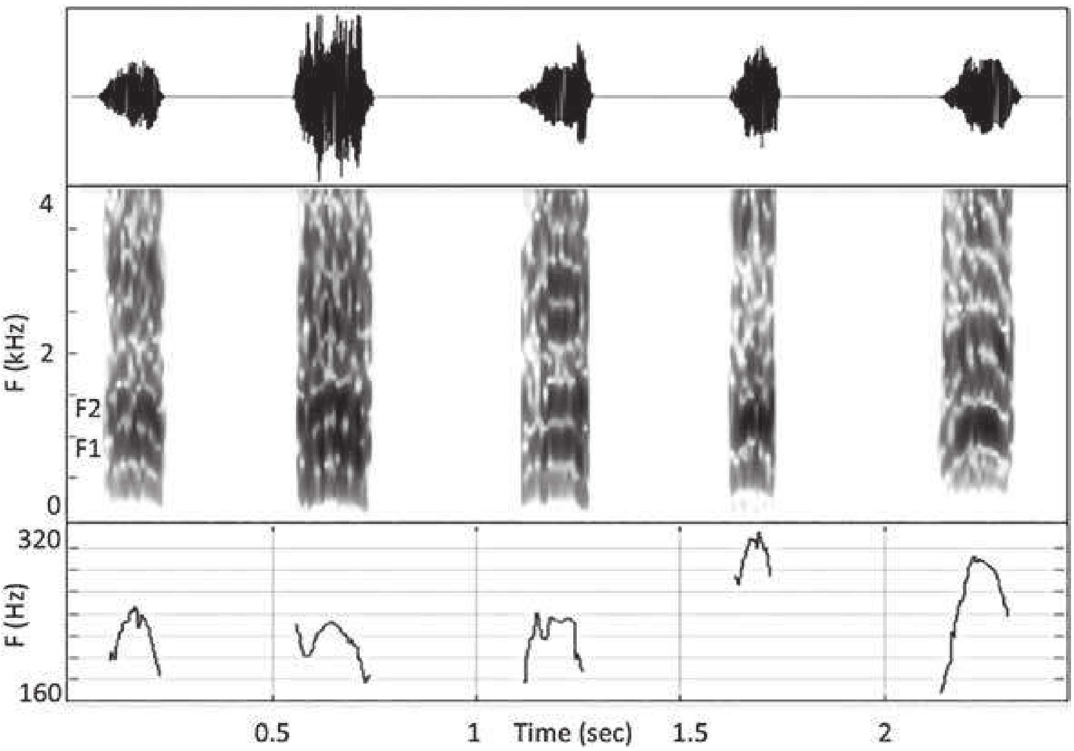
3.2.2 Barks

Barks were recorded in two main contexts – prior to feeding in response to the presence of humans (contact barks) and in response to the presence of sheep (alarm barks). They were not distinguishable by ear, but the analysis did reveal differences in their acoustic structure. The difference between contact and alarm barks is described below. We observed barks to also occur in two other, albeit more rare, instances. One infant (Grimm), produced barks after his mother was removed from the troop due to illness. We deemed these barks also as a form of contact (see Cheney et al., 1996), but were not included in the analysis of the contact barks. The second instance was in response to the alarm wahoos of the nearby olive baboons. As it was not possible within the constraints of this study to determine if our subject group could distinguish between the contact and alarm wahoos of the olive baboons, we did not categorize their response barks as either contact or alarm. Only one adult male, Articho, produced barks (in both the contact and alarm contexts), but this was rare and this vocalization was more typically produced by females, juveniles and even one infant (Grimm). Barks were produced with a rounded 'O' shape mouth.

- *Contact barks*

Acoustic description (see Figure 3): This bark is sharp and clear, with a defined and modulated harmonic structure, and lower signal-to-noise ratio than observed in alarm barks. The F0 of contact barks typically followed a curved temporal pattern, rising in frequency (Hz) from the start of the call before returning to the starting frequency; this curved feature was less pronounced in adult male barks. The barks produced by Grimm after the removal of his mother were shorter (0.12 ± 0.01s) than those he produced prior to feeding (0.18 ± 0.01s), and the F0 was similar.

Figure 3: Contact barks. These five contact barks were produced by an adult male, sub-adult male, sub-adult female, juvenile and infant, respectively. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants (middle panel), and F0 calculated with Praat (bottom panel).



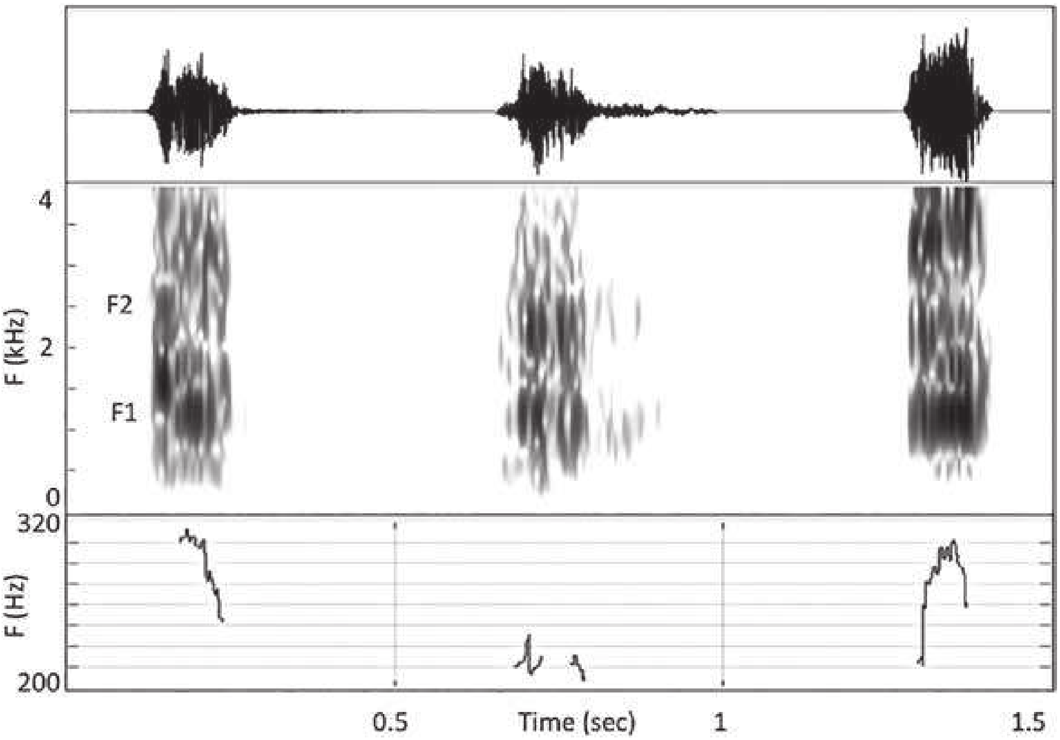
Context & usage: Contact barks were largely produced in the hour prior to feeding when the baboons observed humans leaving the office complex nearby and when the humans were preparing the food. The baboons visually fixated on staff when producing these barks. Barks by one individual could elicit barks in others to create a chorus.

Terminology: Clear bark (*Papio ursinus*: Ey and Fischer, 2011; Fischer et al., 2001b), dog-like bark (all savannah baboon species: Estes, 1992; *P. cynocephalus*: Hall and DeVore, 1965), contact bark (*Papio ursinus*: Cheney et al., 1996; Ey and Fischer, 2011; Fischer et al., 2001a), sharp bark (*P. papio*: Byrne, 1981).

- *Alarm barks*

Acoustic description (see Figure 4): With higher formants, alarm barks have quite the same general acoustical structure as the contact barks describe above; however, this bark type is noisier than the contact barks and less tonal.

Figure 4: Alarm barks. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants and characteristic vertical lines due to low F0 periodicity (middle panel), and F0 calculated with Praat (bottom panel). These three alarm barks were produced by an adult female, a sub-adult male and a juvenile, respectively.



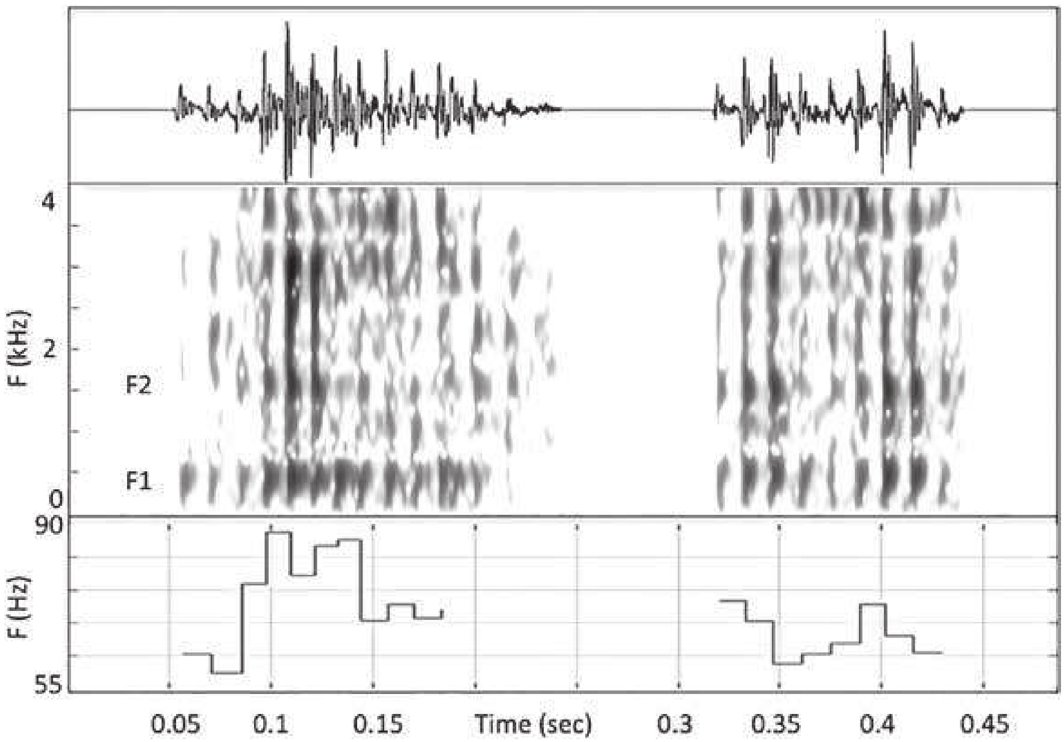
Context & usage: Alarm barks were produced when the sheep were heard approaching, grazing next to and passing by the primate center. Single barks were the norm, although barking bouts (up to 6, with less than 1.5 sec between calls) were recorded. The baboons visually fixated on the sheep, or in the direction from which the sheep could be heard approaching, when barking.

Terminology: Fear bark (*P. ursinus*: Cheney and Seyfarth, 2007), alarm bark (*P. ursinus*: Cheney and Seyfarth, 2007; *P. papio*: Byrne, 1981), cough-bark (*P. anubis*: Ransom, 1981), harsh bark (*P. ursinus*: Fischer et al., 2001a), shrill bark (all savannah baboon species: Estes, 1992; *P. cynocephalus*: Hall and DeVore, 1965; *P. anubis*: Ransom, 1981; Rowell, 1966; *P. ursinus*: Fischer et al., 2001a), sharp bark (*P. papio*: Byrne, 1981).

3.2.3 Threat Grunts

Acoustic description (see Figure 5): Threat grunts are a highly noisy call, with harsh but soft rolling egressive cough-like sounds. There were enough recordings of single call productions to suggest that a call should be considered as the vocalization; however, vocal bouts were still common, although the temporal connection between call units was quite variable. The F0 of this vocalization is low and unstable within each call, but the formants are stable. Although individual threat grunts are produced by sub-adults and adults as a single phase (i.e., continuous production), juveniles typically gave a seemingly double phase grunt, as if the sound hitched during production.

Figure 5: Threat grunts of an adult male. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants and characteristic vertical lines due to low F0 periodicity (middle panel), and F0 computed with our Matlab script (bottom panel).



Context & usage: This vocalization was observed in two contexts. The first of these was in antagonistic situations between adult females, in which the aggressor produced the vocalization. The second context was in response to the sheeps; all sex-age groups produced this vocalization in this context, although it was rarer in adult males and infants. Threat grunts were often observed in conjunction with barks (juveniles, adult females and sub-adult males) and wahoos (adult males only). Two calls were often produced within 1.5 sec before a long pause until the next call.

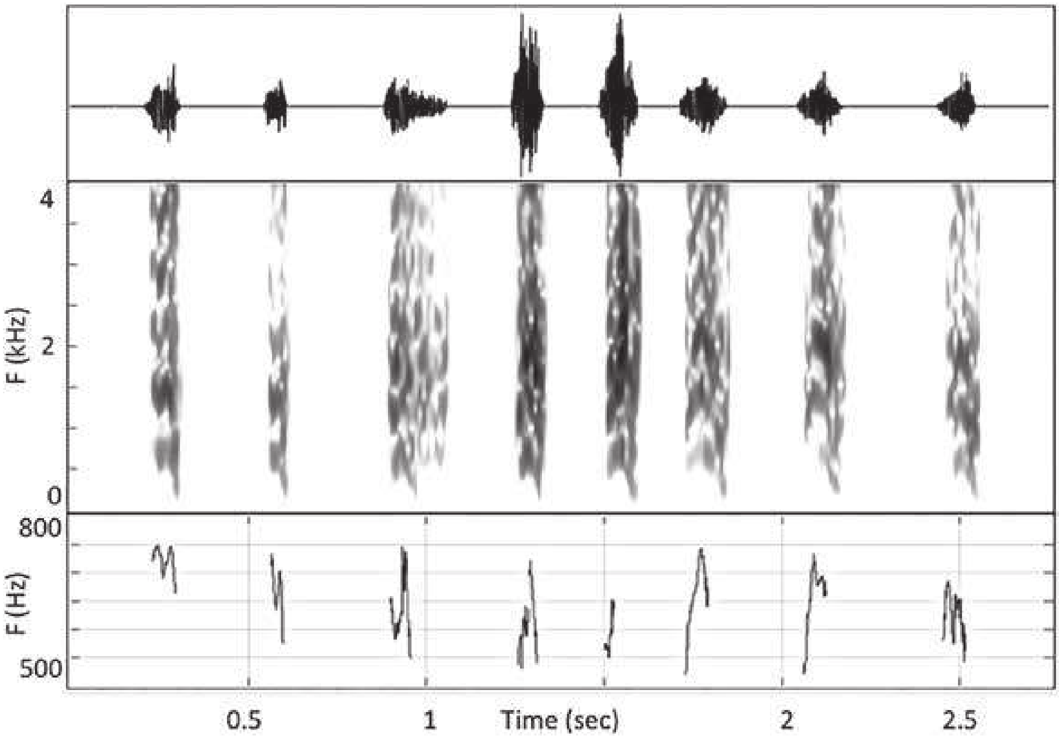
Terminology: Threat grunts (*P. ursinus*: Cheney and Seyfarth, 2007; Engh et al., 2006).

3.2.4 Yaks

Acoustic description (see Figure 6): Yaks have an irregular harmonic structure. The F0 is also modulated, being highly variable within a single call, with a lower frequency at the beginning of the yak than at the end. This vocalization is typically produced as a series of high F0, single phase calls with even temporal distribution, although calling rate can increase with context intensity. Up to 50 yaks in a series were recorded, with calls being considered as part of the same series when produced less than 1.5 sec apart.

Context and usage: This vocalization was produced by individuals being threatened or in distress. The corresponding facial expression involved a strong retraction of the lips. It may be that the call is a form of appeasement, as suggested by Estes (1992). It did not appear to act as a recruitment vocalization. Infants produced yaks when they were rebuffed by their mother and were looking for comfort, often in the form of nursing. Yaks were produced as a long series of calls, but were also given in conjunction with screams and/or moans (infants only) in varying orders and numbers. Context suggested that yak-only series were given in lower intensity situations, especially in comparison to screams. Yaks were produced by adults with the teeth bared and the body often cowed and shoulders hunched, with the tail lowered and ears back. Yaks by infants were not given with the same body posture; instead, infants were usually running after their mothers.

Figure 6: Yaks of an adult female. Audio signal (top panel), wide-band spectrogram (Praat) visualizing the harmonics (middle panel), and F0 calculated with Praat (bottom panel).



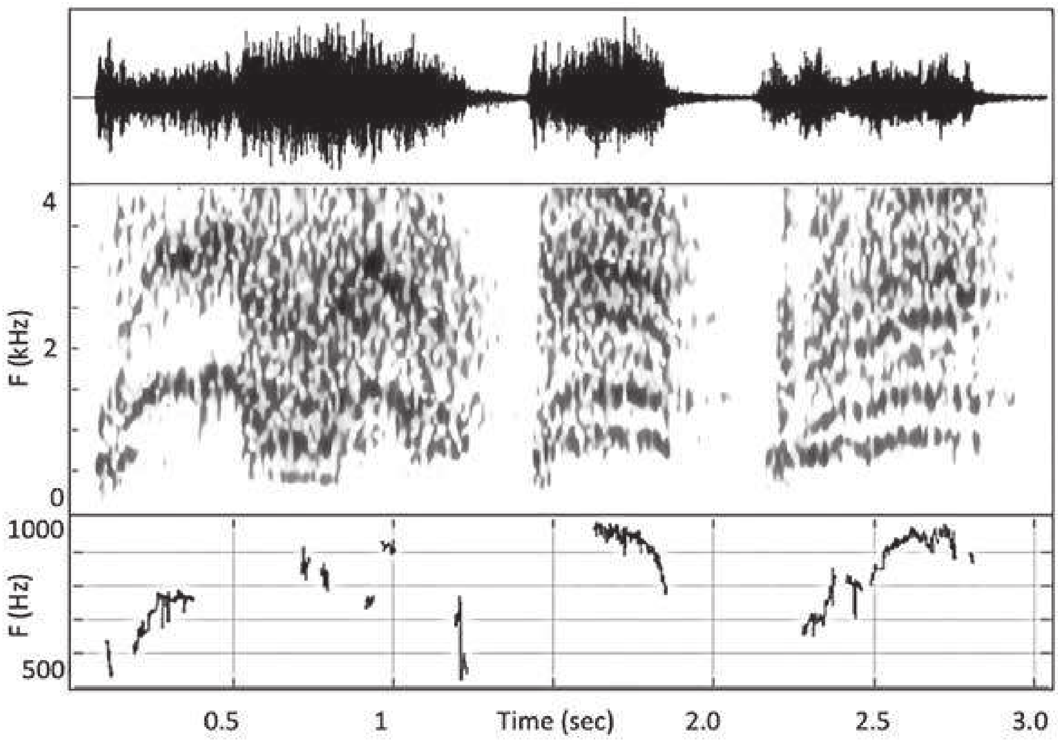
Terminology: Yak/yakking (*P. cynocephalus*: Hall and DeVore, 1965; all savannah baboon species: Estes, 1992), geck (infants only – *P. anubis*: Ransom, 1981; *P. papio*: Anderson and McGrew, 1984; *P. hamadryas*: Ransom, 1981; Smuts, 1985), chirplike clicking (infants only – *P. cynocephalus*: Hall and DeVore, 1965), ick (of the ick-ooer, infants only – all savannah baboon species: Estes, 1992), fear bark (*P. ursinus*: Cheney and Seyfarth, 2007), staccato coughing (*P. hamadryas*: Kummer, 1968), disjointed coughing (*P. hamadryas*: Ransom, 1981; Smuts, 1985), contact call (Rendall et al., 2009).

3.2.5 Screams

Acoustic description (see Figure 7): Screams were highly variable, probably the most variable vocalizations produced by the baboons. Calls could have either harmonics or no clear harmonics, with some recorded instances of calls having alternations of both characteristics. Durations were also variable, ranging from less than a second (quick yelps) to extended calls of over

2s. They could be produced as a single call or as multiple calls within a bout. The high F0 (~1kHz) did not allow for formants to be observed. The maximum frequency observed was very high (approaching 20kHz). Some screams (or scream sections) were noisy and harsh with no clear harmonic structure. Harmonic production could be either clear or mixed with some noise. Inspection of screams found that the baboons could change F0 quite rapidly and dramatically within a call. Screams were considered singular vocalizations that could be produced in bouts. Each call was analyzed separately.

Figure 7: Screams of a sub-adult male. Audio signal (top panel), wide-band spectrogram Praat) showing the harmonics (middle panel), and F0 (bottom panel) calculated with Praat. Note that F0 is too high in this example for visualizing the formants,



Context & usage: Screams were observed in three main contexts: surprise, fights and maternal rejections (i.e., produced by infants when their mother did not allow nursing or clinging). Screams produced when the baboon was surprised by an event, such as a sudden movement or shock, was more a 'yelp'-like sound. Regarding the second context, screams were occasionally produced by the aggressing individual, but it was far more typical for the scream to be produced by the individual being aggressed. Screaming from infants could produce reactions from adults and older juveniles, including grunting and physically comforting; screams due to maternal rebuffs rarely elicited a response from other baboons. These screams were strongly harmonic. Screams were often coupled with yaks and/or moans (infants only) in various combinations (e.g. yak-scream-scream-yak-yak-yak-yak-yak-yak-yak-scream-yak-yak-moan). A single yak often preceded a screaming bout. One sub-adult male baboon (Cloclo) and one juvenile (Feya) would produce a short scream after a single bark at feeding. Screams were produced with the teeth bared and the lips retracted.

Terminology: Scream (*P. anubis*: Ransom, 1981; *P. papio*: Byrne, 1981), screaming (Hall and DeVore, 1965), screeching (Estes, 1992).

3.3 Vocalizations produced by adults and sub-adults

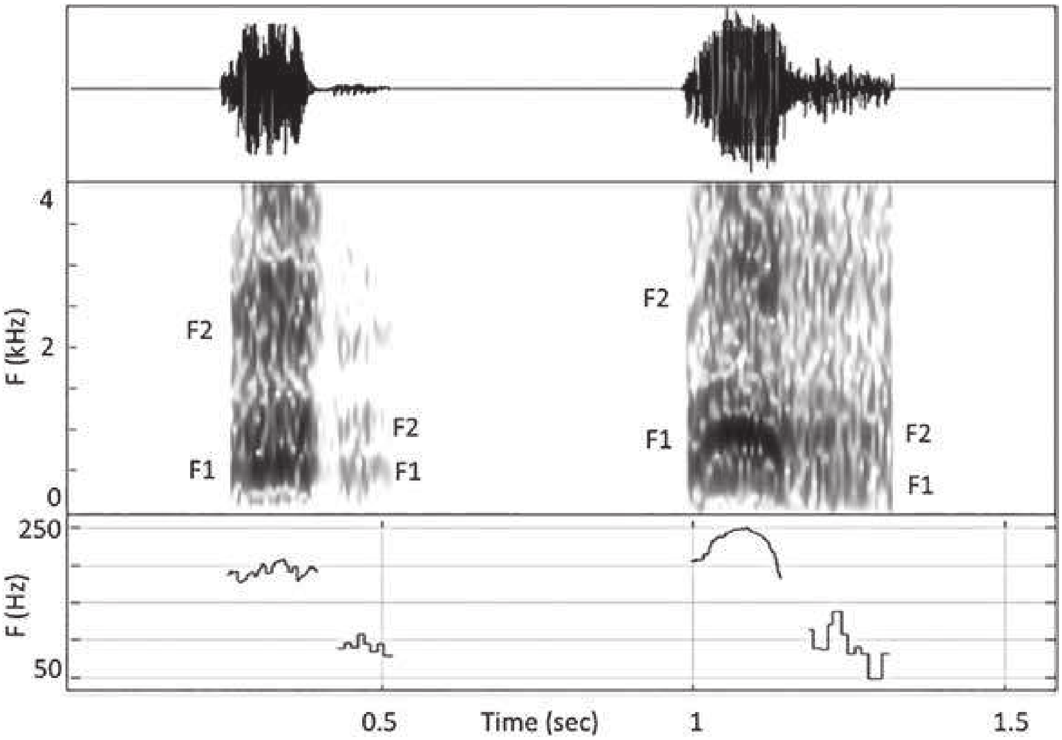
3.3.1 Wahoo

Wahoos in our population were primarily produced in three contexts: in response to the wahoos from *P. anubis* (contest wahoo), prior to feeding in conjunction with barks (contact wahoo) and in response to the sheep (alarm wahoo). The contest wahoos were typically produced in low light, making identification of the vocalizing individual difficult. As we could not be sure in our recordings if any of these vocalizations came from our group of Guinea baboons or the nearby olive baboons, they are not included in our discussion here.

- *Contact wahoos*

Acoustic description (see Figure 8): Wahoos are a two-phase, single call vocalizations with high and low F0 sequences. As with the contact barks, these wahoos had a lower signal-to-noise ratio than those produced in the alarm context. The F0 varies from the 'wa' to the 'hoo', with the latter typically produced with a lower F0.

Figure 8: Contact wahoos of sub-adult males. Audio signal of a wahoo (top panel), wide-band spectrogram (Praat) showing the first two formants (middle panel), and F0 (bottom panel) calculated with Praat for the wa-, and with our Matlab program for the -hoo.



Context & usage: Contact wahoos were typically made by sub-adult males, although occasionally adult females also seemed to give a wahoo instead of a bark. However, it is important to note that while wahoos from adult females were often identified by ear, spectrogram analysis showed that these were more likely to be barks, with the 'hoo' sound being a faint continuation of the exhalation of breath. During production, the mouth was widely opened in an elongated vertical 'O' during the 'wa', before closing to a horizontal opening for the 'hoo'.

- *Alarm wahoos*

Acoustic description (see Figure 9): The 'wa' of alarm wahoos showed some similarities with the alarm barks, in that they were tonal with a large degree of noise. The 'hoo' production was distinct and of longer duration in this context, in comparison to the wahoos produced prior to feeding (Table 2).

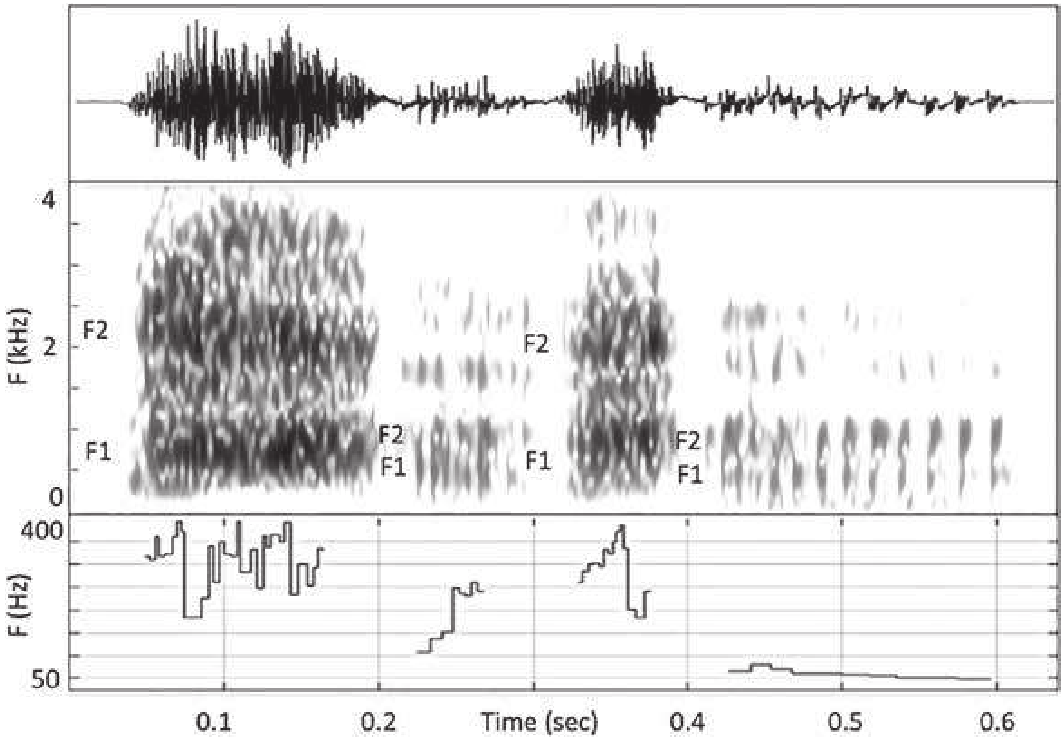
Table 2: Results of the analyzes of the temporal features of each vocalization type for each age-sex category with a useable sample size of ≥10 separate vocalizations. That is, male grunts, two-phase grunts, and roar grunts were not included.

	Sex/age category	**n_v**	**n_c**	**n_i**	**Fmx (kHz)**	**SE**	**C_{DUR} (sec)**	**SE**	**I_{DUR} (sec)**	**SE**	**T_{DUR} (sec)**	**SE**	**C/B**	**SE**
Rhythmic grunts	AM	12	92	3	4.49	764.7	0.11	0.01	0.46	0.06	3.08	0.83	6.9	1.70
	AF	22	150	7	5.75	379.4	0.09	0.01	0.48	0.03	3.75	0.62	7.2	0.73
	SAM	10	22	1	7.47	1325.0	0.08	0.01	0.54	0.06	3.01	1.14	5.5	1.55
	J	10	60	4	7.20	548.3	0.09	0.004	0.59	0.05	3.45	0.70	6.0	0.9
	I	10	21	3	8.69	490.5	0.10	0.01	1.79	0.04	1.98	1.01	2.0	0.80
Barks -Contact	AF	11	n/a	5	19.15	751.2	n/a	n/a	n/a	n/a	0.16	0.01	n/a	n/a
	SAM	10	n/a	3	17.07	883.6	n/a	n/a	n/a	n/a	0.2	0.01	n/a	n/a
	J	12	n/a	6	15.53	886.6	n/a	n/a	n/a	n/a	0.13	0.01	n/a	n/a
	I	10	n/a	2	15.53	1569.8	n/a	n/a	n/a	n/a	0.18	0.01	n/a	n/a
-Alarm	AF	10	n/a	6	19.70	343.8	n/a	n/a	n/a	n/a	0.13	0.01	n/a	n/a
	SAM	10	n/a	3	20.90	425	n/a	n/a	n/a	n/a	0.13	0.00	n/a	n/a
	J	12	n/a	7	19.08	696.9	n/a	n/a	n/a	n/a	0.11	0.01	n/a	n/a
	I	10	n/a	2	20.66	168.3	n/a	n/a	n/a	n/a	0.11	0.01	n/a	n/a
Threat grunts	AF	19	n/a	4	2.93	107.2	n/a	n/a	n/p	n/p	0.08	0.03	n/a	n/a
	SAM	12	n/a	1	2.85	78.7	n/a	n/a	n/p	n/p	0.14	0.01	n/a	n/a
	J	27	n/a	4	18.40	546.1	n/a	n/a	n/p	n/p	0.10	0.01	n/a	n/a
Yaks	AF	10	200	8	19.55	725.5	0.11	0.01	0.37	0.02	14.49	1.06	23.6	9.1
	J	10	212	5	17.03	481.8	0.07	0.01	0.16	0.05	4.72	2.55	19.8	10.7
	I	10	250	4	16.22	564.2	0.04	0.02	0.19	0.03	12.84	3.27	22.9	13.2

	Sex/age category	n_v	n_c	n_i	Fmx (kHz)	SE	C_{DUR} (sec)	SE	I_{DUR} (sec)	SE	T_{DUR} (sec)	SE	C/B	SE
Screams	AM	10	n/a	2	18.01	167.4	n/a	n/a	n/a	n/a	0.77	0.11	n/p	n/p
	AF	18	n/a	7	19.00	404.5	n/a	n/a	n/a	n/a	0.49	0.15	n/p	n/p
	SAM	20	n/a	6	17.68	769.1	n/a	n/a	n/a	n/a	0.85	0.22	n/p	n/p
	J	28	n/a	5	19.22	398.2	n/a	n/a	n/a	n/a	0.64	0.09	n/p	n/p
	I	18	n/a	3	19.99	661.6	n/a	n/a	n/a	n/a	0.72	0.14	n/p	n/p
Wahoo -Contact	SAM -Wa	10	n/a	5	17.13	4020.0	0.16	0.01	n/a	n/a	n/a	n/a	n/a	n/a
	-Hoo	10	n/a	5	10.99	1589.4	0.15	0.01	n/a	n/a	0.31	0.01	n/a	n/a
-Alarm	AM -Wa	12	n/a	3	13.92	1318.8	0.18	0.01	n/a	n/a	n/a	n/a	n/a	n/a
	-Hoo	12	n/a	3	7.41	219.7	0.28	0.02	n/a	n/a	0.45	0.02	n/a	n/a
	SAM -Wa	12	n/a	5	17.30	2436.8	0.16	0.01	n/a	n/a	n/a	n/a	n/a	n/a
	-Hoo	12	n/a	5	8.03	1426.2	0.15	0.01	n/a	n/a	0.3	0.01	n/a	n/a
Copulation grunts	AF	20	177	7	12.49	544.0	0.07	0.003	0.18	0.01	2.04	0.26	8.9	1.09
	SAF	10	59	1	6.60	550.6	0.06	0.003	0.02	0.02	1.31	0.2	5.36	1.0
Chattering	J	10	53	5	3.03	678.2	0.04	0.02	0.37	0.09	4.66	0.54	9.9	2.3
Moan	I	23	n/a	3	6.15	593.1	0.91	0.05	1.78	0.51	14.23	1.85	n/a	n/a

n/a = not applicable; (n_v) = the number of vocalizations/series; (n_c) = the number of individual call units; (n_i) = the number of individual baboons whose calls were used in the analysis; (C_{DUR}) = the duration of each call or phase; (I_{DUR}) = the duration of the interval between two calls in the same bout; (T_{DUR}) = the total duration of a bout; (C/B) = the number of calls per bout; SE = standard error. Age/sex categories: AM – adult males, AF – adult females, SAM – sub-adult males, SAF – sub-adult female, J – juveniles, I – infants. SE – standard error.

Figure 9: Alarm wahoo of an adult male. Audio signal of a wahoo (top panel), wide-band spectrogram (Praat) for visualizing the first two formants (middle panel), and F0 (bottom panel) which was computed with our Matlab program.



Context & usage: Like alarm barks, alarm wahoos were in response to the sound of and/or the presence of sheep. Although wahoos are typically considered as a single call vocalization, a series of three wahoos were observed on a few occasions and double wahoos – with the first wahoo shortened and immediately followed by the second wahoo – were also recorded.

Terminology: This terminology corresponds to both contact and alarm wahoos, as little to no differentiation in names have been noted within the literature. Wahoo bark (*P. papio*: Byrne, 1981), contact bark (*P. ursinus*: Cheney and Seyfarth, 2007; Ey and Fischer, 2011), wa-hoo (*P. anubis*: Ransom, 1981), wahoo (*P. ursinus*: Fischer et al., 2002 [note that the authors differentiate between 'contact', 'contest' and 'alarm' wahoos in terminology]; Kitchen et al., 2003), two phase/d bark (all savannah baboon species: Estes, 1992; *P. cynocephalus*: Hall and DeVore, 1965;

P. hamadryas: Ransom, 1981; Smuts, 1985), type 2 loud call (*P. papio*: Byrne, 1981), loud call (*P. ursinus*: Fischer et al., 2002; Kitchen et al., 2003) bahu bark (*P. hamadryas*: Kummer, 1968), oohu roar (*P. hamadryas*: Kummer, 1968).

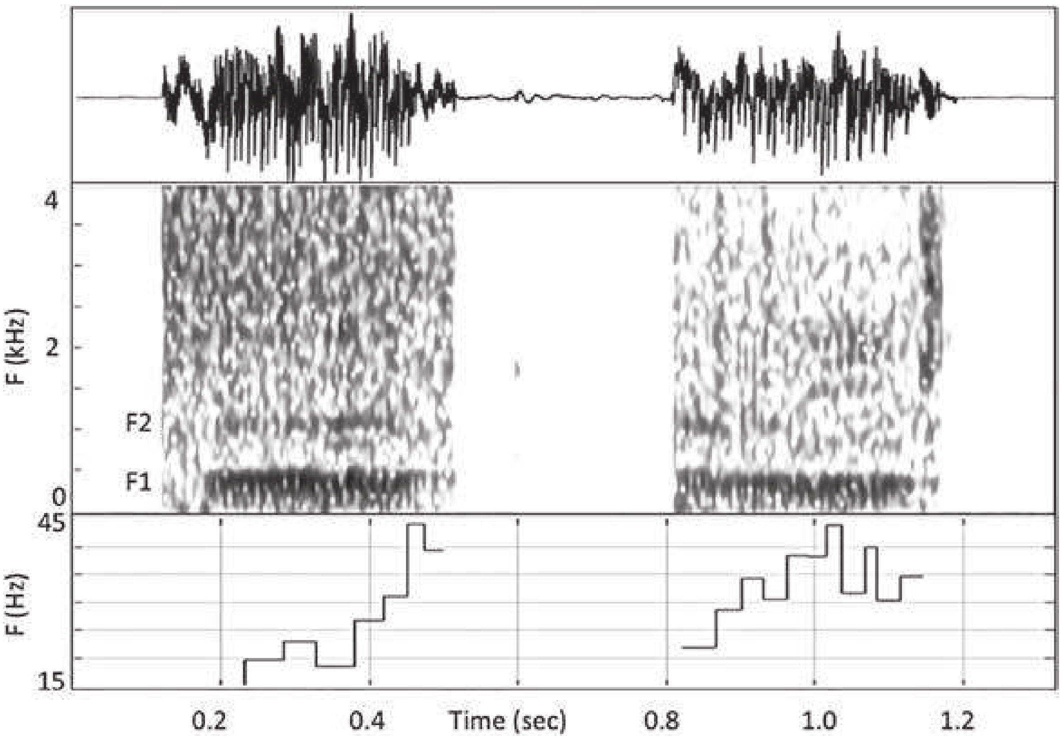
3.3.2 Roargrunts

Acoustic description (see Figure 10): This is a series of loud grunts with a hum-like grunt typically preceding the call, a pause of 5–6 sec and then 4–6 grunts produced in close succession as a crescendo, with a final long grunt or roar, similar to a double wahoo. The call sequence is variable, with the hum difficult to discern or absent, and the concluding roar not always produced. We did not record enough of these vocalizations to determine why there was so much variability in the entire bout. However, the grunts that make up the majority of the vocalization were always present and produced consistently. Although we did not analyze this vocalization due to the small sample size, we did note that the grunts had a low F0 (~30Hz), with F1 typically around 440Hz and F2 at 1.1kHz. Each call within the bout was typically longer (0.34s) than those produced by the adult males during rhythmic grunting (0.11s), although the interval durations were similar (~0.45s). The notable features of this vocalization are the long grunts produced at a slow calling rate (~1.7grunt/s).

Context & usage: Adult males produced this call either prior to feeding or when the sheep were present, suggesting it is in response to high arousal level due to tension.

Terminology: Type 1 loud call (*P. papio*: Byrne, 1981), roargrunt (*P. papio*: Byrne, 1981; Maciej et al., 2013b; *P. anubis*: Ransom, 1981; *P. hamadryas*: Ransom, 1981; Smuts, 1985), hum-roargrunt (*P. anubis*; Ransom, 1971), roaring (all savannah baboon species; Estes, 1992), crescendo of two-phase grunts (all savannah baboon species; Estes, 1992), grating roar (*P. anubis*: Estes, 1992).

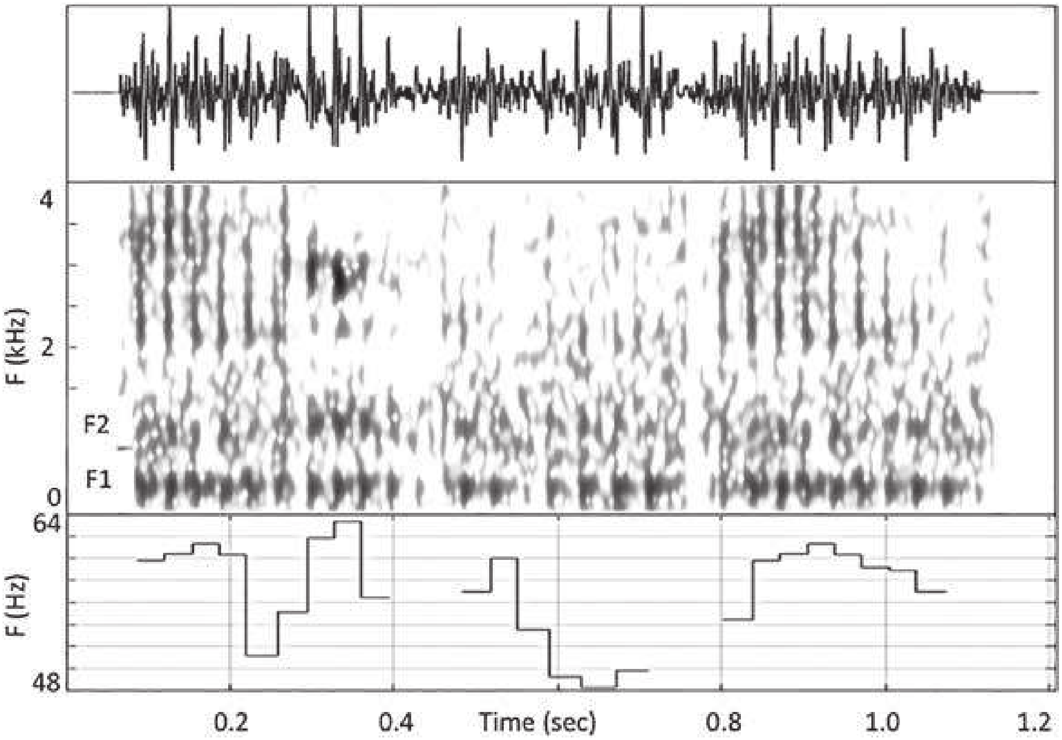
Figure 10: Roar grunt of an adult male. Audio signal (top panel), wide-band spectrogram (Praat) for visualizing the first two formants (middle panel), and F0 (bottom panel) computed with our Matlab program.



3.3.3 Male Grunts

Acoustic description (see Figure 11): This vocalization was particularly difficult to analyze as it was often produced with accompanying acoustic displays that interfered with the recorded signal (see below, 'Context & usage'). Therefore, we only provide spectrograms and audio files (see supplementary material) of prototypical examples of these calls, but no analysis was performed. The vocalization consists of a series of rapidly-produced, short (~0.05sec), breathy, strongly egressed grunts, which form a crescendo and sometimes end in a roar or double wahoo, similar to that heard at the end of some roargrunt sequences.

Figure 11: Male grunt of an adult male. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants and the characteristic vertical lines due to low F0 periodicity (middle panel), and F0 computed with our Matlab program (bottom panel).



Context & usage: This is an adult and sub-adult male vocalization, albeit rarely in the latter ones, and typically performed together with power displays. These displays include fence shaking, jumping and rock throwing, and throwing the head back. Observations were made of both adult and sub-adult males as well as one infant (Grimm), one juvenile/sub-adult (Dan) and some adult females performing these displays without the vocalization or with only a subset of the full vocalization, suggesting that the coordination to do both required development and strength. This vocalization was produced after fights with other males, when the sheep were present for long periods of time, prior to feeding – especially if feeding was delayed – and when the computer systems (see Fagot and Palleressompoule, 2009), to which the baboons usually had access, were blocked. These contexts suggest that this vocalization is associated with high arousal levels and frustration, as well as indicators of male size and strength.

Terminology: Could not accurately determine corresponding vocalizations in other publications but may be the deep grunts described for *P. papio* by Byrne, (1981).

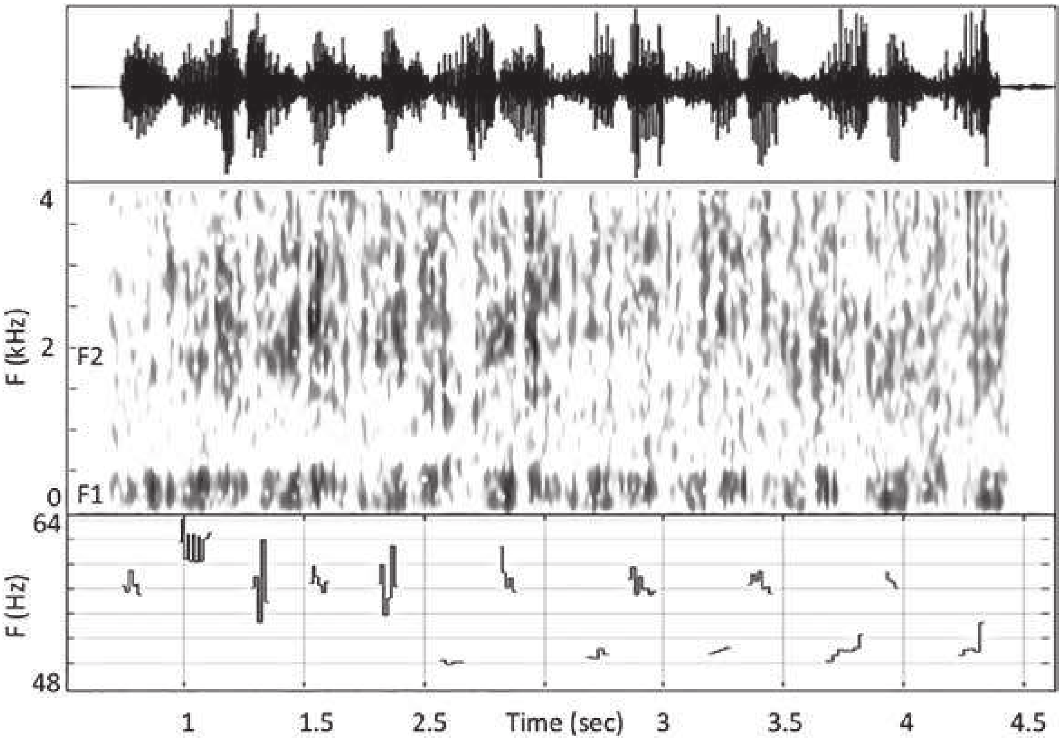
3.3.4 Two-Phase Grunts

Acoustic description (see Figure 12): As we only recorded a few instances of this vocalization, it was not analyzed in any great detail. These grunts were produced as a series, with two grunts paired, i.e., in close temporal proximity with short interval duration (~0.04s) then a longer interval duration (~0.15s) before the next pair. Duration of each pair was 0.4s, with the first grunt longer (~0.27s) than the second (~0.13s). It is therefore recommended that the grunt is analyzed like the wahoo, and considered, as the name suggests, as a two-part call. Due to the production of this vocalization (see below, 'Context & usage'), it is likely to be dismissed as panting. However, the clear formant structure (F1 = ~350Hz, F2 = ~2kHz) and controlled production indicates that this is a vocalization and not a consequence of running. Bouts were long (between 11 and 18 grunt pairs), with the first grunt being typically of a higher F0 (~60Hz) than the second grunt (~50Hz) within each pair.

Context & usage: Two-phase grunts are ingressive-egressive vocalizations, similar to panting. It was only produced by adult males, in contrast to the study by Byrne (1981), who found that all age-sex classes except infants produced this vocalization. The males were observed making this call while being chased by other adult males during fights.

Terminology: Two-phase grunts (*P. papio*: Byrne, 1981), pant-grunt (*P. anubis*: Ransom, 1971) uh-huh (all savannah baboon species: Estes, 1992; *P. cynocephalus*: Hall and DeVore, 1965), grunting (all savannah baboon species: Estes, 1992).

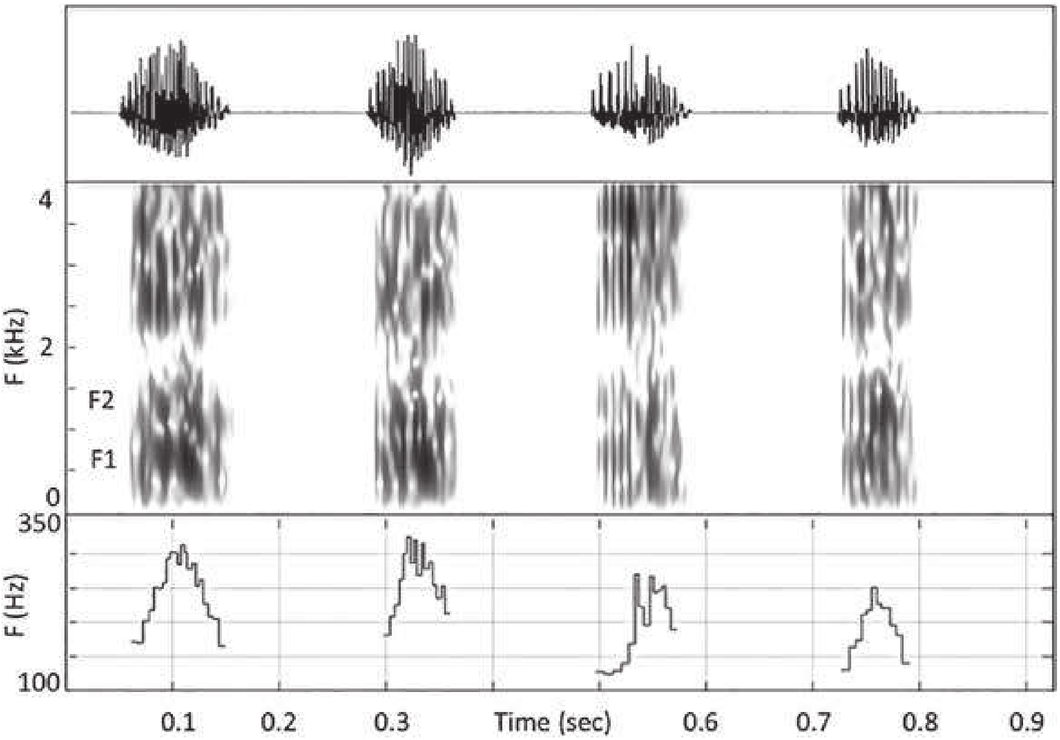
Figure 12: Two phase grunts of an adult male. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants (middle panel), and F0 (bottom panel) computed with our Matlab program.



3.3.5 Copulation Calls

Acoustic description (see Figure 13): Copulation calls are defined by the production of a series of grunt calls (never singular), with fluctuating speed and F0. Egressed grunt-like breaths without formants were occasionally dispersed between the true grunts and/or at the end of the series. Copulation calls were typically tonal.

Figure 13: Copulation calls produced by adult females. Audio signal (top panel wide-band spectrogram (Praat) showing the first two formants (middle panel), and F0 (bottom panel) calculated with Praat.



Context & usage: Adult, sub-adult and even juvenile (rare) females produced this vocalization toward the end of copulation, completing the call while running away from their male partner. It was also observed in one adult female (Mona) while being mounted by other females. The vocalization was preceded by a distinctive facial expression, in which the mouth was rounded into a ‘O’ shape, with the lips slightly pursed. Not all copulations were followed by copulation calls; however, the vocalization was produced more often than it was not and the facial expression was always present regardless of whether or not the vocalization was uttered.

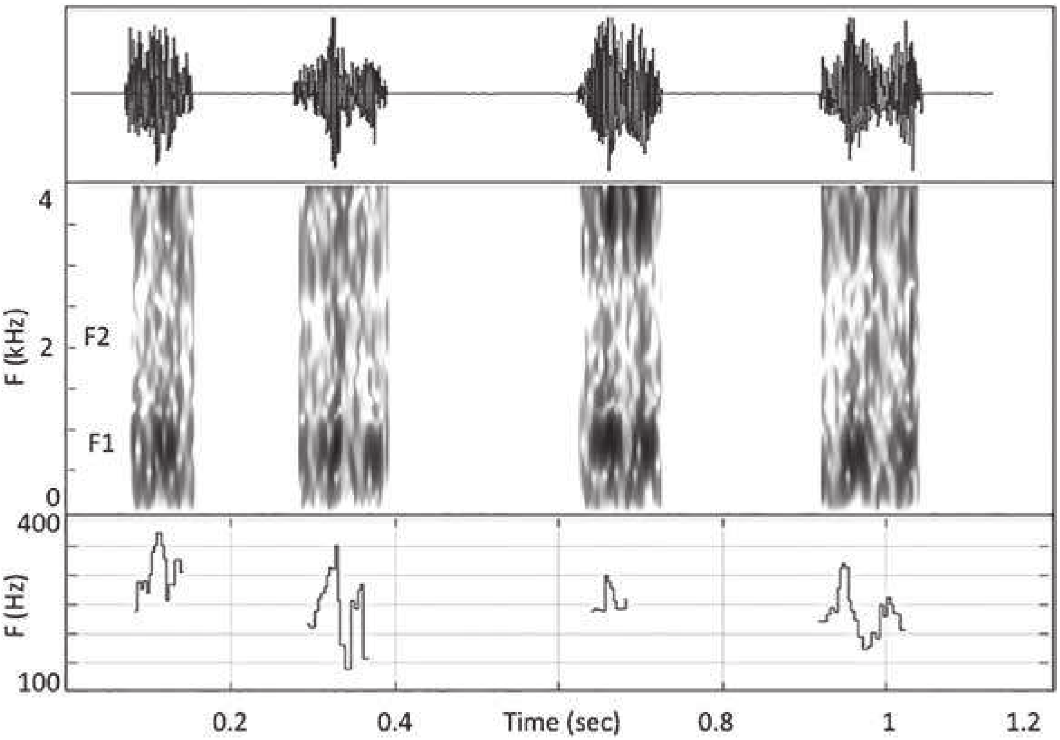
Terminology: Muffled growl (all savannah baboon species: Estes, 1992; *P. cynocephalus*: Hall and DeVore, 1965), copulation grunts/call (*P. papio*: Byrne, 1981; *P. cynocephalus*: Hall and DeVore, 1965; Semple et al., 2002).

3.4 Vocalizations produced by infants and juveniles

3.4.1 Chatterings

Acoustic description (see Figure 14): Chattering is a series of unevenly spaced single phased calls, which have a chuffing-like sound, possibly ingressive-egressive due to the production method (see below, 'Context & usage'). The vocalization is quite soft in amplitude and not strongly harmonically structured (i.e., noisy). Formants and F0 were often difficult to discern, particularly in infants who produced much noisier calls than older juveniles.

Figure 14: Chatterings produced by a juvenile. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants (middle panel), and F0 (bottom panel) computed with our Matlab program.



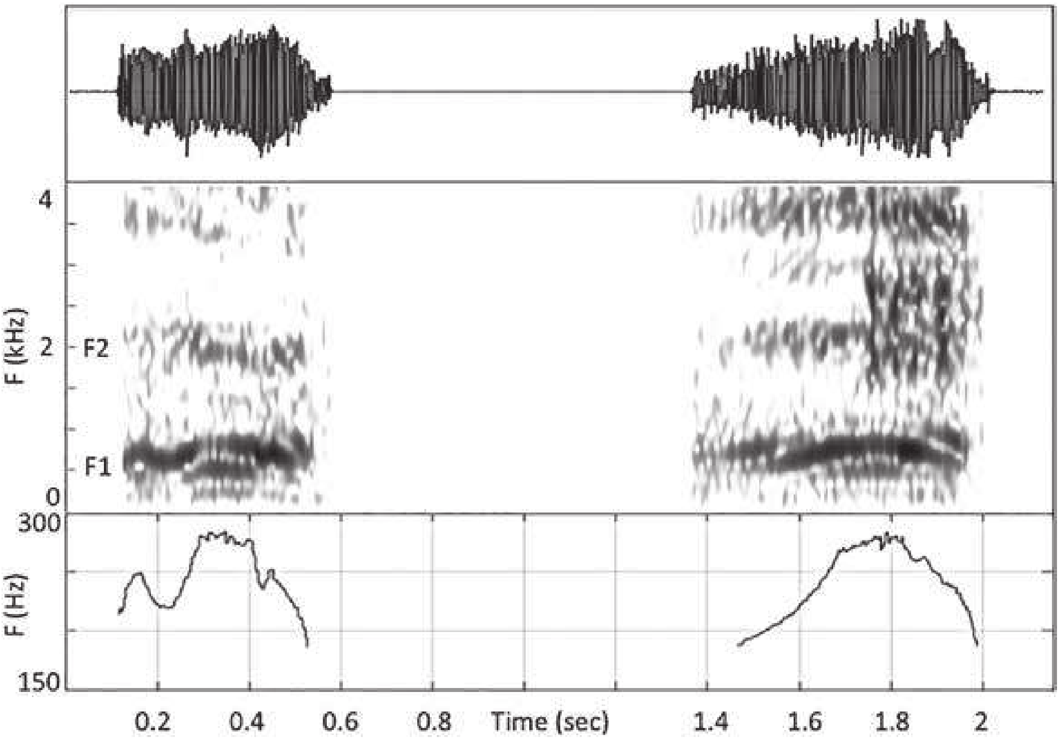
Context & usage: Chattering was used during play behavior, usually while running.

Terminology: Chattering (*P. ursinus*: Estes, 1992), panting (*P. anubis*: Ransom, 1981; *P. hamadryas*: Ransom, 1981; Smuts, 1985).

3.4.2 Moans

Acoustic description (see Figure 15): Moans are a single phase, single call vocalization. The call has a strong tonal structure with even formants and a gently arching, high F0. It sounds similar to a sheep vocalization.

Figure 15: Moans produced by an infant. Audio signal (top panel), wide-band spectrogram (Praat) showing the first two formants (bottom panel), and F0 (bottom panel) calculated with Praat.



Context & usage: This vocalization was only observed to be produced by infants, usually in response to maternal rebuff or in distress situations. As with yaks, moans seemed to be produced when the mother was walking, not allowing her infant to be fed and hold on. Series of moans were observed; this seemed to be an extension of singular calls. Moans were often accompanied by yaks, to produce the 'ick-ooer' sound described by Hall and DeVore (1965). However, we noted that several yaks often preceded the moan. Occasionally, moans were accompanied by a scream after their production, but the two were not linked in the same way as the yak-moan sound.

Terminology: Ooer (of the ick-ooer – *P. cynocephalus*: Hall and DeVore, 1965), moan (*P. anubis*: Ransom, 1981; *P. hamadryas*: Ransom, 1981; Smuts, 1985), infant moan (*P. papio*: Byrne, 1981).

4. Formant analyses

4.1 Methods for formant analyses conducted on vocal categories

Formant analyses were performed for several classes of vocalization, including the grunts (two-phase grunts excluded), barks, wahoos, yaks and copulation calls. Vocalizations of infants and juveniles, and adult screams were not considered for these analyses because of their F0, sometimes approaching 1 kHz. The method used for formant analysis is explained in details in the supplementary material of Boë et al. (2017). For these analyses, the part of the vocalizations containing formants were grouped into one file per vocalization type (e.g., bark). The grunt file included the rhythmic, threat and roar grunts. These different types of grunts were grouped together because they were highly similar in their formants. The two-phase grunts were not included in the grunt file, because they differed slightly from the other grunts regarding their formants (see Figure 12). The bark files grouped the alarm and contact barks, and the wa- and -hoo files also grouped the alarm and contact wahoos. To limit the perturbation due to noise and to maximize the reliability of the LPC results and achieve the clearest possible characterization of the vocalizations, formant analyses were performed using frames from 0.5 to 2 seconds long, so that each frame encompassed several utterances. It was done with successive frames operating as a sliding window overlapping by 50%, and the results and subsequent processings were based on the frame outputs from this LPC processing. The frame database was then filtered to further control for detection errors, and all the frames missing F1 or with F1 or F2 values greater than 3 standard deviations from the means of their categories were eliminated from the dataset (see below). Also, F0 was measured in the same frames using autocorrelation and peak-picking. The detailed corpus characteristics and LCP settings are provided in Table 3. Interested readers are referred to Boë et al. (2017) for an in-depth discussion of our choice of variables, regarding for instance the number of poles.

Table 3: Corpus characteristics and LPC settings.

	Grunt ♂ ♀	Wa- ♂	-hoo ♂	Cop ♀	Bark ♀	Yak ♀
CORPUS						
N baboons	13	3	3	8	11	10
N vocalizations	522	69	69	124	116	504
Total duration (s)	65	11	15	10	29	69
Mean duration (ms)	125	159	219	81	250	137
LPC SETTINGS						
N poles	60	30	60	60	30	60
Frame duration (s)	1	1	1	0.5	1	2

4.2 Results of formant analyses conducted on vocal categories.

The acoustic results regarding F0 and the first two formants are reported in Table 4 for each class of vocalizations. Table 4 reveals that the baboons produced high- (i.e., ♂ wa-, ♀ bark, and ♀ yaks), and low vowel-like sounds (i.e., ♂ and ♀ grunts, ♂ -hoo, ♀ copulation calls), which are characterized by F1 formants in the high and low ranges, respectively. Table 4 also demonstrates the production of front and back vowel-like sounds, characterized by F2 formants in the high (♂ -wa, ♀ bark) and low ranges (♂ and ♀ grunts, ♂ -hoo, ♀ copulation call, and ♀ yak). We have no space here to present our analyses on formants in more details. However, note that this data set was analyzed in depth by Boe et al. (2017). Examining these vocalizations through modeling of their maximal acoustic space based on anatomical measures of the baboon's vocal tract, Boe et al. (2017) demonstrated that these vocalizations share the F1/F2 formant structure of the human [ɨ æ ɑ ɔ u] vowels. From these results, we can conclude that the baboons can produce several vocalic qualities differentiated by their formant structures, and that these structures are characteristic properties of vocalizations produced in distinct social contexts, or for different functions.

Table 4: Acoustic results obtained for vocalizations that could be analyzed for the first two formants and F0. The numbers in bracket indicate the standard deviations.

	Grunt ♀	**Grunt** ♂	**Wa-** ♂	**-hoo** ♂	**Cop** ♀	**Bark** ♀	**Yak** ♀
CORPUS STATISTICS							
Total nb of frames	39	76	18	26	36	50	19
ACOUSTIC RESULTS							
F1 (Hz)	476	392	948	552	583	1044	916
	(31)	(63)	(70)	(82)	(93)	(89)	(140)
F2 (Hz)	1440	1219	2165	1025	1211	2685	1500
	(129)	(137)	(112)	(66)	(119)	(121)	(116)
F0 (Hz)	64	61	417	121	133	431	—
	(20)	(20)	(105)	(37)	(56)	(45)	—

5. Discussion

5.1 On the Guinea baboon's vocal repertoire

We observed and recorded twelve vocalizations, easily distinguishable by both ear and production/acoustic characteristics, produced by our group of baboons. Two calls, the bark and the wahoo, showed slight differences in acoustic features when produced in different contexts (contact and alarm). Interestingly, more types of vocalizations were given by adult males in our study than any other sex/age category (Table 1) and constituted the second largest proportion of recorded vocalizations despite the small sample size. Eleven of the vocalizations in our repertoire had certainly been reported previously, either for Guinea baboons or other baboon taxa, but we could not find a clear analogy to the male grunt vocalization in any of the baboon vocal literature. It is a possibility that Byrne (1981) had referred to this vocalization as the 'deep grunt' but with only a description of "long, low pitched grunt, fluctuating in pitch and volume. Adult males only (?)" (p. 287) it is difficult to be sure.

Seven of the vocalizations we describe are short distance communications; that is, their production did not allow for long-distance detection. The baboons showed a large range of F0 production, from around 40 Hz for grunts to up to 1 kHz for screams. Feeding time and the occasional presence of sheep elicited the greatest variety of calls (barks, wahoos, threat grunts [in response to the sheep, only], roargrunts and male grunts) of any major contexts recorded. In regard to feeding, due to the captive environment, we are able to report the first known transfer of two vocalizations (barks and wahoos) to a new context in this species. It is known that baboons will use barks and wahoos to contact conspecifics when moving through dense vegetation (Cheney et al., 1996; Rendall et al., 2000) but this is the first time these calls have been reported to be used as a contact with caretakers.

We observed that some vocalizations could elicit vocal responses from conspecifics but found little evidence of communicative volleys between individuals. Some vocalizations (rhythmic grunts, screams, yaks, threat grunts, chattering and moans) could be directed towards specific baboons but they rarely elicited a vocal response. The bark or wahoo of one individual when observing (either visually or through auditory means) the approach of a human at feeding time or the sheep would often result in the production of these calls (usually barks) from other baboons. However, these calls were directed at external stimuli. Wahoos produced by adult males at night are known to create volleys whereby males from different groups produced wahoos back and forth (Anderson and McGrew, 1984; Byrne, 1981). We observed this occurring between our Guinea baboons and the olive baboons at night, but never just between the males within our group, and certainly the alarm wahoos in response to sheep never elicited a vocal response from the olive baboons. Although screams have been considered a recruitment call (e.g., in infants, Rendall et al., 2009), we found no particularly strong evidence to support this hypothesis; only some of the screams from infants and juveniles resulted in a vocal response (rhythmic grunts) or physical approach from adults (most screams were produced during conflicts and may better act as appeasement). However, it is important to note that rhythmic grunts directed towards individuals could elicit rhythmic grunts. For example, adult males grunting towards infants or juveniles would sometimes get grunts in return as the two animals approached each other. Hugging baboons would also often grunt. More research is required to determine the specific cues in the initial vocalization of one baboon that elicits the same vocal response, particularly when it is directed specifically to a conspecific rather than an external stimulus, in another baboon.

One vocalization that is produced by all age- and sex-groups is the yak. The term 'yak' has been typically used for the adult production of the infant/juvenile 'geck' vocalization. 'Geck' or 'gecker' is a common infant primate vocalization (see Jacobus and Loy, 1981; Patel and Owren, 2007) and is usually not produced by adults within these other species. Despite the alternative naming, it has long been suspected that the 'geck' and the 'yak' in baboons are equivalent. Certainly, we noted them in similar contexts, although infants have additional contexts (e.g., maternal rebuff). Our analysis suggests that the calls are the same, with acoustic structure differences due to the caller (i.e., age, size, development etc.). Meanwhile, after infancy the moan vocalization is no longer produced and chattering disappears at some point during the sub-adult stage.

In the literature, wahoos are typically differentiated between those made by adult females, juveniles and even sub-adult males from those produced by adult males, which are considered more stereotyped (e.g., Byrne, 1981; Fischer et al., 2002). These studies suggest that in adult female wahoos the 'hoo' is often missing or inaudible. We propose that these calls are more likely to be barks. Also, as the 'wa' of the wahoo is suspected to be ingressive (Gustison et al., 2012; also, personal observation – authors CK, TL and YB) but a bark is egressive, it is unlikely that these are the same vocalization and we therefore suggest that they should be more clearly differentiated in repertoires.

In a more general perspective on baboon's repertoire, detailing the vocal ethogram of Guinea baboons is a first step in better understanding the differences between the baboon taxa. It is important that full ethograms, including those from infants and juveniles, are reported for the other species so that we can better understand how the socio-ecological conditions, morpho-physiological and behavioral differences, as well as geographical variations, have affected vocal use for these closely related taxa.

5.2 On language evolution

The main strength of our study is the description of the acoustic parameters of the baboon's vocal productions, and the description of the ethological context in which these vocalizations were produced. In doing so, we followed a strategy which is not so different from language studies that try to map the acoustic features of the vocal production to meanings, as for example when phonology distinguishes the American words boat (/bot/) and bat (/bæt/) exclusively through the distinction between the /o/ and /æ/ vowel phonemes they contain. This approach suggests at least three lines of discussion regarding the evolution of language.

First, we note that the vocal repertoire of Guinea baboons is of a limited size (see McComb and Semple, 2005) for a species with a large social group size (Patzelt et al., 2011). The small repertoire of twelve vocalizations we report here is further constrained by the individual call types. That is, grunt-based vocalizations account for over half of the Guinea baboons' vocal repertoire. However, it appears that the baboons can increase their repertoire through the use of variability. Variability in vocal production occurred through changes of F0, tempo (calling rate), call duration, number of calls within a bout, and the combination of different vocalizations (e.g., the scream-yak-moan sequences of infants, bark-screams, double wahoos). More work is needed to identify whether the variability we observed in vocal production convey specific meanings. Addressing this question would require, for instance, comparing behavioral responses to long yak- or grunt series, in comparison to short series. The variations we observed in the baboon's vocalizations suggest that a first stage in language evolution might have been to introduce variations in the production and use of a limited set of vocal units, rather than expanding the number of different vocalizations. Considering context and variation within vocalizations may be essential to determine how nonhuman primates expand their limited repertoire to communicate with conspecifics, and to document the emergence of language.

Second, the analysis of the baboons' vocalizations has shown that several of them contain formants, and that these formants differ from one class of vocalization to the other (see Table 4). It has long been thought that nonhuman primates are incapable of producing sets of vowels-like sounds due to anatomical limitations (in particular, a too high larynx, Lieberman et al., 1969). The observation that baboons produce different vocal qualities, in different ethological contexts, shows that nonhuman primates can produce contrasting vowel qualities despite a high larynx (see Fitch et al., 2016 for converging results). This finding suggests homologies between baboons' vocalizations and human vowel systems, and more generally, that spoken languages could have evolved from an ancient vocal proto-system already present in our last common ancestor with baboons (Boë et al. 2017).

Third, Table 4 also reveals an interesting finding on language evolution. This table shows that F0 varied greatly both across (e.g., 64Hz for grunt 1 and 417 Hz for the wa (of wahoos)), and even within the vocalizations (417Hz for the wa- and 121Hz for the -hoo of the wahoos). In human languages, formants vary independently from laryngeal frequency, and the fundamental frequency of the baboons' vocal production was not as stable as found in speech. This finding suggests that the production of F0 and of formants could have been entangled during the early stages of language evolution. Clearer dissociations would have emerged later in the hominid lineage.

In summary, the data presented in this paper have two main functions. Firstly, this work aimed at serving as a reference guide for students of baboons' vocalizations and those interested in the communication systems of nonhuman animals. Furthermore, in documenting these aspects of baboons' vocal communication, this study also provides hypotheses on the emergence of speech. We believe that there is much to learn on these two aspects if this approach is replicated in other nonhuman primate species.

Supplementary material

Illustrative examples of the different vocalizations can be found at https://osf.io/nr2ye/

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Appendix 1. Glossary of terms used

Term	Meaning
Vocalization	Type of vocal production, with series of calls taken into account (i.e., copulation call). That is, a vocalization can either be comprised of a single call (e.g. wahoo) or a bout of calls which can be temporally connected (less than 1.5s apart) to be within the same vocalization (e.g. rhythmic grunts which are never produced as a single call)
Call	Individual unit within a vocalization (i.e., single grunt within a series).
Calling rate	Speed of call production within the bout (number of calls/s).
F0	Fundamental frequency. Measured in Hz.
Formant F1 F2	Acoustic resonances (first and second) of the vocal tract, affected by the position of the tongue, mouth cavity and lips. Measured in Hz.
Maximum frequency	The highest frequency (Hz) observable in our spectrograms.
Noise	Lacking harmonic structure
Harmonics	The simple periodic waves which make up the vocal signal, in which the F0 is the first harmonic and each subsequent harmonic repeats at the interval of the F0.

Appendix 2. List of the subjects involved in this study, their housing group, sex and age in months at the start of the study, as well as classification

The broad age classifications used (adult: 7+ years; sub-adult: 5–7 years; juvenile: 2–5 years; infant: < 2 years) were based on studies conducted on *P. cynocephalus* (Altmann et al., 1981) and *P. hamadryas* (Sigg et al., 1982). * indicates that these individuals moved up an age category during this study (age category given is that at the start of the study). ^ indicates that most of the vocalizations recorded for these individuals were after the move to the next age category. ° indicates that these individuals were selected for formant analysis. Any vocalizations of these individuals recorded around the time frame of their transition to the next category were carefully considered before analysis classification but we largely kept to the definition of category class.

Name	Group	Sex	Age (months)	Category
Pipo °	1	M	156	Adult
Vivien °	1	M	94	Adult
Bobo	1	M	73	Sub-adult
Dan	1	M	53	Juvenile*
Felipe	1	M	27	Juvenile
Filo	1	M	22	Infant*^
Grimm	1	M	12	Infant
Harlem	1	M	2	Infant
Kali °	1	F	204	Adult
Brigitte °	1	F	199	Adult
Michelle °	1	F	199	Adult
Mona °	1	F	186	Adult
Atmosphere	1	F	174	Adult
Petoulette °	1	F	162	Adult
Romy	1	F	149	Adult
Uranie °	1	F	104	Adult
Violette °	1	F	92	Adult
Angele	1	F	88	Adult
Arielle °	1	F	82	Sub-adult*
Dream	1	F	51	Juvenile*
Dora	1	F	49	Juvenile
Ewine	1	F	37	Juvenile
Fana	1	F	30	Juvenile
Feya	1	F	25	Juvenile
Flute	1	F	24	Juvenile
Hermine	1	F	6	Infant
Articho	2	M	82	Sub-adult*^
Barnabe	2	M	74	Sub-adult
Cloclo	2	M	66	Sub-adult
Cauet	2	M	65	Sub-adult
B06 °	3	F	332	Adult