

Acoustic Variability and Individual Distinctiveness in the Vocal Repertoire of Red-Capped Mangabeys (*Cercocebus torquatus*)

Hélène Bouchet, Catherine Blois-Heulin, and
Anne-Sophie Pellier
Université de Rennes 1

Klaus Zuberbühler
University of St Andrews

Alban Lemasson
Université de Rennes 1 and Institut Universitaire de France

Acoustic variability and individual distinctiveness of vocal signals are expected to vary with both their communicative function and the need for individual recognition during social interactions. So far, few attempts have been made to comparatively study these features across the different call types within a species' vocal repertoire. We collected recordings of the six most common call types from 14 red-capped mangabeys (*Cercocebus torquatus*) to assess intra- and interindividual acoustic variability, using a range of temporal and frequency parameters. Acoustic variability was highest in contact and threat calls, intermediate in food calls, and lowest in loud and alarm calls. Individual distinctiveness was high in contact, threat, loud and alarm calls, and low in food calls. In sum, calls mediating intragroup social interactions were structurally most variable and individually most distinctive, highlighting the key role that social factors must have played in the evolution of the vocal repertoire in this species. We discuss these findings in light of existing hypotheses of acoustic variability in primate vocal behavior.

Keywords: individual identity, acoustic variability, call function, vocal repertoire, nonhuman primate

Animal vocal signals often have multiple functions that sometimes interfere with one another. Calls can carry information about external events (chickens: Evans & Evans, 2007; mammals: Macedonia & Evans, 1993; Campbell's monkeys: Ouattara, Lemasson, & Zuberbühler, 2009; chimpanzees: Slocombe & Zuberbühler, 2005), the caller's internal state (squirrel monkeys: Fichtel, Hammerschmidt, & Jürgens, 2001; tree shrews: Schehka & Zimmermann, 2009; elephants: Soltis, Leong, & Savage, 2005), or the caller's identity (Price, Arnold, Zuberbühler, & Semple, 2009). Individual differences in vocalizations can reflect physical characteristics, such as the caller's age, sex, or body size (primates: Ey, Pfefferle, & Fischer, 2007; horses: Lemasson, Boutin, Boivin, Blois-Heulin, & Hausberger, 2009; dogs: Riede & Fitch, 1999), but also social factors, such as group membership (mouse lemurs:

Braune, Schmidt, & Zimmermann, 2005; chimpanzees: Crockford, Herbinger, Vigilant, & Boesch, 2004; jays: Hopp, Jablonski, & Brown, 2001), kinship (killer whales: Miller & Bain, 2000; macaques: Rendall, Rodman, & Emond, 1996), position in the hierarchy (baboons: Fischer, Kitchen, Seyfarth, & Cheney, 2004), or social bonding (budgerigars: Brown & Farabaugh, 1997; Campbell's monkeys: Lemasson & Hausberger, 2004; starlings: Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995).

To date, few attempts have been made to systematically study acoustic variability and identity cues across the different call types within a species' repertoire (skuas: Charrier, Jouventin, Mathevon, & Aubin, 2001; mouse lemurs: Leliveld, Scheumann, & Zimmermann, 2011; Campbell's monkeys: Lemasson & Hausberger, 2011; baboon: Rendall, Notman, & Owren, 2009). Nonetheless, a number of mutually nonexclusive hypotheses have been proposed to explain the possible selective pressures that may have favored the evolution of acoustic variability and identity cues in animal signals.

First, the *social function* hypothesis states that there is a positive relation between a call's relevance during social interactions and its morphological complexity. Snowdon, Elowson, and Roush (1997), for example, predicted higher levels of acoustic variability for calls functioning in intragroup social interactions, such as affiliative or threat calls, compared to socially less targeted calls, such as alarm calls or intergroup loud calls. Recent support for this hypothesis has come from research on Campbell's monkeys, which has revealed higher levels of acoustic variability and a greater number of call variants in contact than alarm calls (Lemasson & Hausberger, 2011). Concerning individual distinctiveness, Charrier et al. (2001) suggested that calls used in social interactions were individually more distinctive than calls used for other

Hélène Bouchet, Catherine Blois-Heulin, and Anne-Sophie Pellier, Department of Animal and Human Ethology, Université de Rennes 1, Paimpont, France; Klaus Zuberbühler, Department of Psychology, University of St Andrews, St Andrews, Scotland, United Kingdom; Alban Lemasson, Department of Animal and Human Ethology, Université de Rennes 1 and Institut Universitaire de France, Paris, France.

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Correspondence concerning this article should be addressed to Hélène Bouchet, UMR6552 EthoS—Éthologie animale et humaine, Université de Rennes 1—CNRS, Station Biologique, 35380 Paimpont, France. E-mail: helene.bouchet@yahoo.fr

purposes, as individual discrimination is important during intra-group social interactions. Support for this idea comes again from Campbell's monkeys, where contact calls contained more reliable identity cues than alarm calls (Lemasson & Hausberger, 2011), a pattern also found in birds (skuas: Charrier et al., 2001).

Second, the *distance communication* hypothesis states that there is a relation between individual acoustic distinctiveness and the typical distance of a caller relative to the targeted listeners (i.e., long- vs. short-distance communication; Marler, 1967). The key argument is that, if animals are out of visual range, the acoustic channel becomes the only modality for individual recognition, suggesting that individual distinctiveness should be high. Also, acoustic identity cues are more sophisticated and reliable in species where parents and offspring have difficulties in finding each other (colonial vs. semicolonial vs. solitary nesting species—swallows: Leonard, Horn, Brown, & Fernandez, 1997) and in species experiencing frequent separations (non-nesting vs. nesting species—seals: Insley, 1992; penguins: Jouventin & Aubin, 2002). Accordingly, the general prediction is that calls that function in long-distance communication should be individually more distinctive than calls used for short-range communication, which can benefit from additional visual and olfactory cues. Support for this hypothesis has been provided by Mitani, Gros-Louis, and Macedonia (1996), who have demonstrated that male chimpanzee pant-hoots, used to communicate to spatially separated individuals, encode higher degrees of individuality (i.e., high interindividual and low intraindividual variability) than pant-grunts, used in short-range to mediate dominance relationships among group members. Likewise, individual distinctiveness has been demonstrated in the long-distance calls of various other taxa (guenons: Arnold & Zuberbühler, 2008 and Gautier & Gautier-Hion, 1977; geese: Hausberger, Richard, Black, & Quris, 1994; horses: Lemasson et al., 2009; elephants: McComb, Reby, Baker, Moss, & Sayialel, 2003; langurs: Wich, Koski, de Vries, & van Schaik, 2003).

Third, the *structure-affective processing* hypothesis states that there is a relation between the acoustic properties of a call, its impact on the receiver's affective state, and its degree of individual distinctiveness. This hypothesis is based on arguments made by Owren & Rendall (1997 & 2001), who distinguish two vocal tactics used by callers to influence receivers: 1) direct effects of the acoustic features of a vocal signal to alter attention, arousal, and affect in listeners; 2) indirect effects of a vocal signal in eliciting conditioned (affective) responses in listeners, resulting from past interactions. The first notion is based on the observation that some calls have peculiar morphological features, such as sharp onsets, high-amplitude noise, repeated energy pulses, or frequency and amplitude fluctuations, which tend to be perceived as intrinsically obnoxious, at least by humans. Examples are distress calls and some predator alarm calls. At the same time, such structures are not suitable for conveying individual distinctiveness. The second notion ("affect-conditioning") assumes a Pavlovian conditioning process during which previously neutral calls become associated with positive or negative "affect" or some similar underlying psychological experience. The argument here is that learning is facilitated by calls with tonal and harmonically rich structures, or by calls with diffuse spectra but still regularly patterned structures (i.e., formants). Examples are contact and threat calls. These types of structures, in turn, are well suited for conveying identity cues. Support for the *structure-affective processing* hypothesis has been

provided by Rendall, Owren, and Rodman (1998); Rendall et al. (2009) and Leliveld et al. (2011) for rhesus macaques, chacma baboons, and gray mouse lemurs, respectively.

In this study, we investigated the acoustic variability and the potential for identity coding across the main call types of the vocal repertoire of red-capped mangabeys (*Cercocebus torquatus*). Red-capped mangabeys are an appropriate model to study social influences on acoustic variability because they live in large multimale and multifemale groups, in which individuals frequently interact in affiliative and agonistic ways (Gautier-Hion, Colyn, & Gautier, 1999; Gust, 1994; Jones & Sabater Pi, 1968). They also rely heavily on vocal signals to communicate in their natural habitat, the dense African rainforests (Gautier-Hion et al., 1999). Previous research has already shown that this species possesses a rich vocal repertoire with a multilevel organization (units—calls—sequences) with a capacity to convey a range of information (Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010).

We focused on six frequent call types associated with different social functions, as judged by the most frequent context of production (Bouchet et al., 2010): long-distance loud calls, alarm calls, food calls (two types), threat calls and contact calls. We measured the same set of temporal and frequency parameters in all call types and conducted comparisons within and between callers. We also determined which acoustic parameters accounted for individual distinctiveness across call types. The *social function* hypothesis predicted that the level of acoustic variability and the degree of individual distinctiveness were related to the call's importance during social interactions (i.e., high for contact and threat calls, intermediate for food calls, and low for alarm and loud calls). The *distance communication* hypothesis predicted that the loud and alarm calls were individually more distinctive than the other call types. The *structure-affective processing* hypothesis, finally, predicted that calls with sharp onsets, high-amplitude noise, repeated energy pulses, or frequency and amplitude fluctuations (in our case loud, alarm and food calls) were less individually distinctive than other calls.

Methods

Subjects and Housing Conditions

Fourteen adult red-capped mangabeys (*Cercocebus torquatus*) were observed ($N = 7$ males: 8, 12, 14, 15, 18, 18, 23 years; $N = 7$ females: 4, 6, 8, 12, 16, 21, 26 years), all captive-born. They were housed at the Station Biologique de Paimpont (Université de Rennes 1, France) in outdoor (around $20 \text{ m}^2 \times 4\text{m}$)—indoor ($10 \text{ m}^2 \times 3\text{m}$) enclosures enriched with litter and perches. They were kept under various social conditions (single, male only, female only with offspring, pairs, single male multifemale, and multimale and multifemale). Group sizes ranged from 1 to 7 individuals, including offspring. Subjects obtained fruit and vegetables in the morning, and commercial monkey chow in the afternoon. Water was available ad libitum.

Data Collection

Observations were conducted on males between February and April 2006, and on females between February and April 2008. As

we intended to perform an in-depth structural analysis of man-gabey vocalizations, captivity offered good opportunities to obtain high quality recordings at close range under controlled conditions.

Observations consisted of 15-min all occurrence samples of any vocal utterance produced by the focal subject ($N = 77$ hrs, range: 4.5–7.5 hrs per individual). Subjects were observed in random order and observation sessions were homogeneously distributed over the time from 09:00 to 18:00 h local time. Call recordings were made outdoors, using a Sony ECM-672 directional microphone connected to a digital stereo recorder (Marantz PMD660 for females, Sony DAT TCD-D100 for males—sampling rate: 44.1 kHz, amplitude resolution: 16 bits). In total, $N = 6,629$ calls (range: 88–1,016 calls per individual) were collected.

Data Analysis

The species' vocal repertoire has been described earlier, listing a total of eight call types (Bouchet et al., 2010). For this study, we focused on the six most common call types (see Figure 1), covering the full range of social function. We did not manage to collect all call types from all 14 individuals, but both sexes contributed to the data set (for call types which were shared). Young and old individuals were equally represented (young females ≤ 6 years; old females ≥ 16 years; young males ≤ 14 years, old males ≥ 18 years). The repertoire under investigation consisted of two sex-specific call types and four shared call types: 1) male “Whoop-Gobble” loud call, produced during intergroup choruses, in association with alertness and behavioral displays. The call has been

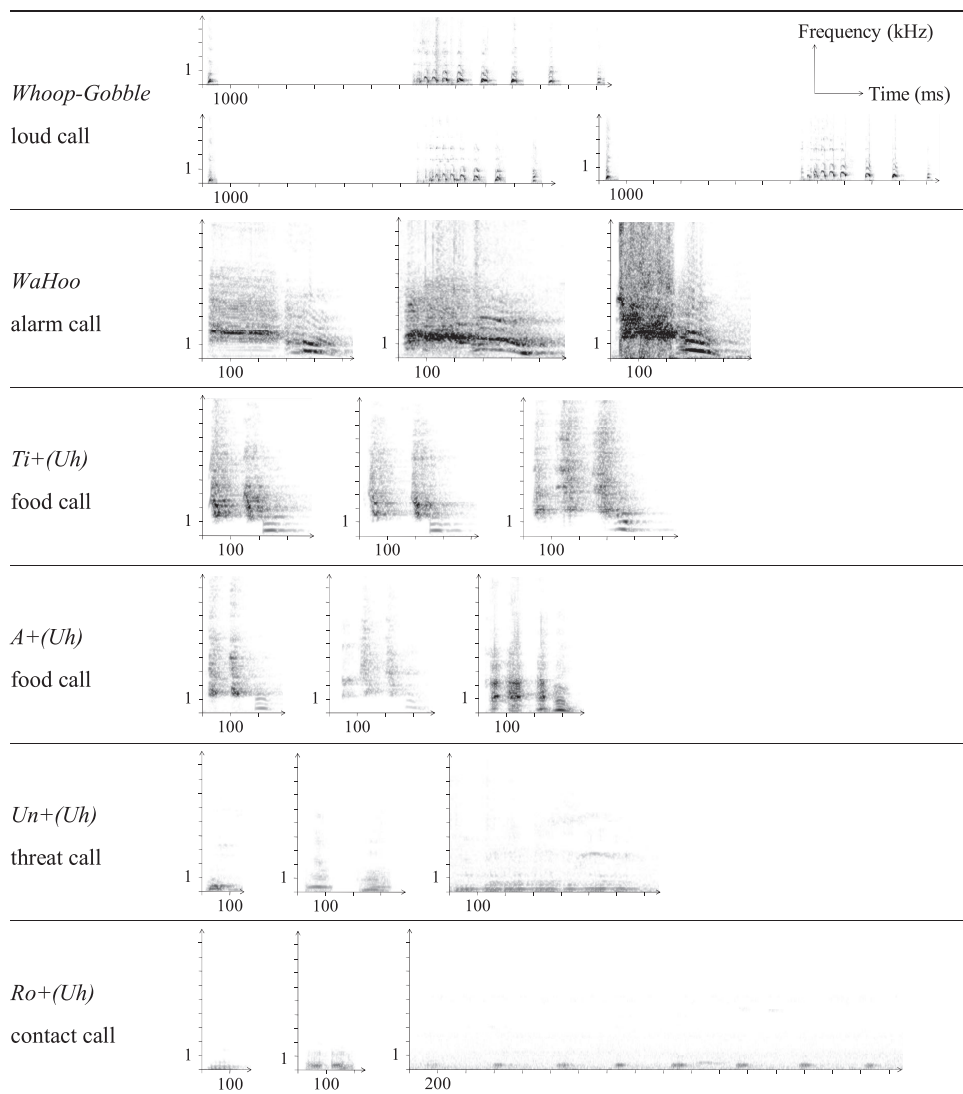


Figure 1. Sonograms illustrating interindividual variability of the six call types. For each call type, the three exemplars shown were produced by three different individuals. Call types are named onomatopoeically according to their component units (Bouchet et al., 2010). The optional repetition of the principal unit (i.e., unit type introducing the call) is symbolized by the sign ‘+’ while the facultative presence of an Uh unit is symbolized by writing it in brackets.

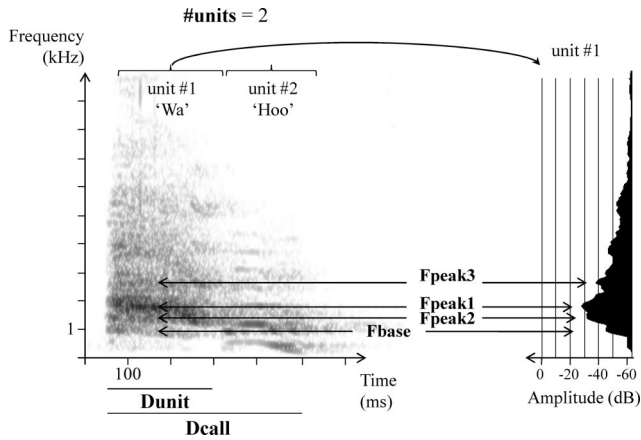


Figure 2. Acoustic measuring of calls. Parameters measured: call duration (Dcall), number of units (#units), duration of the first unit (Dunit), base frequency of the first unit (Fbase), and peak frequencies of the first unit (Fpeak1, Fpeak2, Fpeak3) (see the Methods section for definitions). Exemplar shown: WaHoo call produced by a male.

said to function in intergroup spacing and intragroup cohesiveness; 2) male and female “WaHoo” alarm call, produced when unusual events occurred. This call can warn conspecifics about the imminence of a danger; 3–4) two food calls, the female-specific “Ti+(Uh)” call and the shared “A+(Uh)” call, both produced in response to food. The latter was associated with competition over food. The calls inform conspecifics about the presence of food and may function to announce food ownership; 5) male and female “Un+(Uh)” threat call produced by aggressors during agonistic interactions. This call appears to function as an agonistic display; 6) male and female “Ro+(Uh)” contact call, produced mostly in conjunction with affiliative interactions but also during feeding or in association with male sexual displays. This call appears to function in making or maintaining contact with conspecifics.

Spectrographic illustrations were made using a Fast-Fourier Transform function (1024-pt FFT length containing 256 samples and zero padding, incremental step: 32 pt) using ANA acoustic software (Richard, 1991) implemented on Linux.

Table 1
Call Types Characteristics and Sample Size

Acoustic parameter	Call type Function	Whoop-Gobble loud call	WaHoo alarm call	Ti+(Uh) food call	A+(Uh) food call	Un+(Uh) threat call	Ro+(Uh) contact call
	<i>N</i> ind	5 ♂	6 ♂ 2 ♀	6 ♀	2 ♂ 7 ♀	6 ♂ 5 ♀	7 ♂ 7 ♀
	<i>N</i> calls	30 (3–10)	75 (5–10)	60 (10)	76 (3–10)	88 (4–10)	134 (4–10)
Call							
	Duration (ms)	11,518 ± 2,803	461 ± 97	217 ± 104	276 ± 121	218 ± 234	1,927 ± 3,288
	Number of units	15.6 ± 5	2 ± 0	2.7 ± 1	3.3 ± 1.5	2.7 ± 2.7	6.9 ± 9.9
First unit	Unit type	‘Whoop’	‘Wa’	‘Ti’	‘A’	‘Un’	‘Ro’
	Duration (ms)	211 ± 57	241 ± 55	80 ± 13	71 ± 26	74 ± 28	75 ± 27
	Base frequency (Hz)	315 ± 45	1,202 ± 233	1,609 ± 298	1,224 ± 230	156 ± 53	207 ± 57
	Peak frequency 1 (Hz)	317 ± 51	1,682 ± 520	2,813 ± 1,262	1,655 ± 845	368 ± 334	385 ± 116
	Peak frequency 2 (Hz)	803 ± 218	1,708 ± 597	3,016 ± 1,403	2,118 ± 826	331 ± 241	291 ± 169
	Peak frequency 3 (Hz)	703 ± 130	2,268 ± 788	2,939 ± 1,411	2,113 ± 677	384 ± 337	548 ± 328

Note. *N*ind = Number of individuals of each sex contributing to the data set; *N*calls = Number of samples measured (min–max per individual). For each acoustic parameter: $MEAN_{intra} \pm SD_{intra}$: intraindividual mean and associated standard deviation (see the Statistical Analysis section for definitions).

Calls differed in the number of units they contained (see Struhaker, 1967 for definition of “unit”). We thus performed measurements both at the call and unit level (focusing on the first unit only, in case of multiples). As our sample contained both noisy and tonal acoustic structures, with little to no frequency modulation, we focused on seven acoustic parameters that were shared by all call types and have been used in previous studies on vocal variability and individual distinctiveness: call duration (Dcall), number of units (#units) (see also Insley, 1992; Schehka & Zimmermann, 2009), duration of the first unit (Dunit), base frequency of the first unit (Fbase, i.e., lowest-pitched reinforced frequency measured in the middle of the frequency band), and peak frequency of the first unit (i.e., frequency at maximum energy, measured on the power spectrum) (see also Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002; Charrier, Mathevon, & Jouventin, 2003a; Charrier & Harcourt, 2006): Fpeak1, the frequency of the first peak amplitude; Fpeak2, the frequency of the second peak amplitude; Fpeak3, the frequency of the third peak amplitude (see Figure 2). While the three temporal parameters were measured on the spectrogram (i.e., frequency plotted against time) of the call, the four frequency parameters were measured on the averaged energy spectrum (i.e., amplitude plotted against frequency) calculated on the entire length of the first unit (see Figure 2). Sampling rates were adjusted according to the parameter measured (d: 44,100 Hz, $F > 1,000$ Hz: 22,050 Hz, $F < 1,000$ Hz: 11,025 Hz) in order to achieve maximum resolution (respectively 0.7 ms, 22 Hz and 11 Hz). Signals with excessive background noise were excluded from analyses. To achieve a balanced data set, we randomly selected a maximum of 10 exemplars per call type and individual, that is, $N = 463$ calls total (see Table 1).

Statistical Analysis

For each of the five acoustic parameters, across all call types, we computed: (a) interindividual means ($MEAN_{inter}$ calculated over the whole set of calls of a given type) and standard deviations (SD_{inter} calculated over the whole set of calls of a given type); (b) intraindividual means ($MEAN_{intra}$ calculated by averaging individual means) and standard deviations (SD_{intra} calculated by averaging the SD of every individual’s set of calls, and totaling it with the SD calculated over the individual means values); (c)

coefficients of variation, both interindividually ($CV_{inter} = 100 \times SD_{inter}/MEAN_{inter}$) and intraindividually ($CV_{intra} = \text{mean of individual CV values}$; with for each individual, $CV = 100 \times SD/MEAN$); (d) potential for individual identity coding (PIC), an index that measures the relative interindividual variability (Robisson, Aubin, & Brémond, 1993) ($PIC = CV_{inter}/CV_{intra}$). A PIC value greater than 1 suggests that the given parameter could potentially be used for individual recognition. PIC greater than 1 suggests increasingly higher degrees of reliability for individual recognition. We also computed, for each call type separately: (e) the coefficient of variation, both interindividually ($CV_{mean_{inter}}$) and intraindividually ($CV_{mean_{intra}}$) ($CV_{mean} = CV$ averaged over the seven acoustic parameters); (f) the potential for individual identity coding (overall $PIC = CV_{mean_{inter}}/CV_{mean_{intra}}$).

We first compared the acoustic variability across the different call types to test whether call types differed in their overall level of inter- and intraindividual variability (Friedman tests on CV_{inter} and CV_{intra} values). Second, we performed comparisons between call types concerning their degree of individual acoustic distinctiveness, by testing whether call types differed in their overall potential for identity coding (Friedman tests on PIC values) and by performing analyses of variance to test for interindividual differences. To this end, we conducted a Principal Component Analysis (PCA) with Varimax rotation to summarize the seven acoustic variables and to take into account their natural covariation. We retained the same number of principal components (PC) for every call type to maintain comparability, that is $N = 3$ PC (as the associated Eigenvalues were >1 in most cases), and considered acoustic variables with factor loadings $> |0.5|$ as explanatory. Then, for each call type, we performed a MANOVA (multivariate analysis of variance) followed by, for each of the 3 PC, a one-way ANOVA (type III) on the PC scores computed for each call, with *caller identity* as the fixed factor. The proportion of significantly different pairs of individuals out of all possible pairs was assessed from post hoc multiple comparisons LSD tests. Lastly, for each call type, we estimated the proportion of pairs of individuals significantly differing on at least one out of the 3 PC. Finally, we investigated which acoustic parameter was responsible for individual distinctiveness in each call type. We compared PIC values for each of the seven acoustic parameters in each call type, and also tested whether some parameters had a higher potential for identity coding than others whatever the call type (Friedman tests on PIC values). Furthermore, we compared the proportion of significantly different pairs of individuals out of all possible pairs (assessed from the post hoc multiple comparisons LSD tests described above) between call types for principal components whose interpretation (made from the acoustic variables' factor loadings) was similar.

As the analyses above were not systematically performed on the same individuals with the exact same number of calls per individual (because some individuals rarely or never produced certain call types), this may lead to a bias in the results with some individuals or age/sex groups being overrepresented in the dataset. We therefore extracted, for each dyad of call types, a subsample from the full data set so that the same individuals contributed with the same number of calls (see Table 2). We then computed, for each call type separately, the coefficient of variation, both interindividual ($CV_{mean_{inter}}$) and intraindividual ($CV_{mean_{intra}}$), as well as the potential for individual identity coding (overall $PIC = CV_{mean_{inter}}/CV_{mean_{intra}}$). We then compared whether these values differed

between dyads of call types in the same way as they did when using the entire data set.

Statistical analyses were performed using SPSS 17.0 and Microsoft Excel. All tests were 2-tailed and we set significance at $p \leq .05$.

Results

The six call types under investigation exhibited distinctive acoustic features and differed in their acoustic variability and individual distinctiveness (Table 1; Figure 1).

Level of Variability Throughout the Repertoire

The overall level of structural variability varied among the six functionally different call types (Figure 3a). Intraindividual acoustic variation differed significantly between call types (Friedman test on CV_{intra} values: $\chi^2 = 22.92$, $df = 5$, $p < .001$), being lowest in the loud and alarm calls ($CV_{mean_{intra}} < 12\%$), followed by the two food calls ($23\% < CV_{mean_{intra}} < 26\%$), and the threat and contact calls ($CV_{mean_{intra}} > 32\%$) (Figure 3a). Similarly, the level of interindividual variation differed significantly between call types (Friedman test on CV_{inter} values: $\chi^2 = 26.35$, $df = 5$, $p < .001$). Interindividual variability was lowest in the loud and alarm calls ($CV_{mean_{inter}} < 17\%$), intermediate in the two food calls ($26\% < CV_{mean_{inter}} < 28\%$), and highest in the threat and contact calls ($CV_{mean_{inter}} > 57\%$) (Figure 3a).

Dyadic comparisons of call types performed on subsamples of the main data set (same individuals, same number of calls per individual) led to the same conclusion: both intra- and interindividuality ($CV_{mean_{intra}}$ and $CV_{mean_{inter}}$) were lowest in the loud and alarm calls, followed by the two food calls, and then the threat and contact calls (see Table 2).

Degree of Individual Distinctiveness Throughout the Repertoire

The degree of individual acoustic distinctiveness varied among the six functionally different call types (Figure 3b). Each call type possessed an acoustic structure capable of encoding individual identity as judged by their overall PIC, which was greater than 1 in all cases. Accordingly, multivariate analyses of variance revealed significant interindividual differences in all call types (MANOVA: see Table 3). However, coding was more reliable for some call types than others (Friedman test on PIC values: $\chi^2 = 17.45$, $df = 5$, $p = .004$) (see Figure 4). Indeed, the overall potential for individual identity coding was lowest in the two food calls (overall $PIC < 1.12$), intermediate in the loud and alarm calls ($1.34 < \text{overall PIC} < 1.36$), and highest in the threat and contact calls (overall $PIC > 1.67$) (Figure 3b). Likewise, the proportion of significantly different pairs of individuals out of all possible pairs (assessed from post hoc pairwise comparisons LSD tests following the analyses of variance performed on the PC scores for each of the 3 PC) was higher in the contact (91.2%), threat (74.5%), loud (90%) and alarm (82.1%) calls than in the two food calls (respectively 46.7% and 66.7%) (see Table 3).

Dyadic comparisons of call types performed on subsamples of the main data set (same individuals, same number of calls per individual) led to the same conclusion: individual distinctiveness (overall PIC) was lowest in the two food calls, intermediate in the

Table 2

Dyadic Comparisons, With Equal Sample Sizes, of the Overall Level of Intra- and Interindividual Variability and Potential for Identity Coding of the Six Call Types

Call type Function	WaHoo alarm call	Ti+(Uh) food call	A+(Uh) food call	Un+(Uh) threat call	Ro+(Uh) contact call
<i>Whoop-Gobble</i> loud call	Nind = 4♂ N = 27 (4–10)	Nind = 0	Nind = 1♂	Nind = 5♂ N = 30 (3–10)	Nind = 5♂ N = 24 (3–10)
CVmean _{inter}	12.87	—	—	14.35	15.14
CVmean _{intra}	10.39	—	—	44.75	40.74
Overall PIC	1.24	—	—	10.65	11.21
	1.32	—	—	29.34	24.25
		—	—	1.35	1.53
		—	—	1.35	1.68
<i>WaHoo</i> alarm call		Nind = 2♀ N = 15 (5–10)	Nind = 1♂2♀ N = 18 (3–10)	Nind = 5♂2♀ N = 53 (4–10)	Nind = 6♂2♀ N = 69 (4–10)
CVmean _{inter}		13.07	30.87	14.77	26.24
CVmean _{intra}		12.75	30.95	17.65	58.81
Overall PIC		1.02	1.00	13.11	33.04
				1.35	1.78
				1.35	1.44
<i>Ti+(Uh)</i> food call			Nind = 6♀ N = 53 (4–10)	Nind = 5♀ N = 38 (5–10)	Nind = 6♀ N = 60 (10)
CVmean _{inter}			28.05	25.41	27.57
CVmean _{intra}			27.17	24.76	45.44
Overall PIC			1.03	1.03	26.26
					39.18
					25.78
					28.89
<i>A+(Uh)</i> food call				Nind = 2♂5♀ N = 50 (3–10)	Nind = 2♂7♀ N = 76 (3–10)
CVmean _{inter}				27.09	50.30
CVmean _{intra}				24.04	35.42
Overall PIC				1.13	1.42
					1.12
					2.49
<i>Un+(Uh)</i> threat call					Nind = 6♂5♀ N = 82 (4–10)
CVmean _{inter}					56.47
CVmean _{intra}					59.23
Overall PIC					34.11
					33.07
					1.66
					1.79

Note. Nind = Number of individuals of each sex contributing to the data set; N = Number of samples measured (min–max per individual).

loud and alarm calls, and highest in the threat and contact calls (see Table 2).

Acoustic Parameters Reliable for Individual Identity Coding

Some acoustic parameters encoded individual identity more reliably than others (PIC values, Figure 4), but it was not possible to find one key parameter that was systematically more reliable than others, whatever the call type (Friedman test on PIC values: $\chi^2 = 9.64$, $df = 6$, $p = .141$). For all call types, the frequency parameters (Fbase, Fpeak1, Fpeak2 and Fpeak3) appeared to play a key function in individual recognition ($1.0 < \text{PIC} < 1.8$; Figure 4). In the principle component analysis, the frequency parameters consistently associated with the second and the third Principal Components, whatever the call type, while the associated PC scores varied significantly among individuals and allowed to discriminate between 40% or more of all possible pairs (for at least one of the two PC for every call type: ANOVA and post hoc pairwise comparison LSD tests: see Table 3).

The six call types differed when it came to identifying the most reliable parameters for individual identity coding. Two patterns were observed. For the two food calls, the most reliable parameter for individual recognition was a frequency feature (according to the PIC value, Figure 4). In addition, the principal component that

discriminated best between pairs of individuals (i.e., PC II) was associated with frequency parameters (Fbase and Fpeak1 in both cases, but also Fpeak3 in the case of the call type ‘Ti+(Uh)’) (ANOVA and post hoc pairwise comparison LSD tests: see Table 3). Conversely, for the loud, alarm, threat, and contact calls, the most reliable parameter for individual recognition was a temporal feature (according to the PIC values—except for the loud call; Figure 4). In addition, the principal component that discriminated best between pairs of individuals (i.e., PC I) was associated with temporal parameters (Dcall in all cases, but also #units and/or Dunit depending on the call type; ANOVA and post hoc pairwise comparison LSD tests: see Table 3). Finally, only in the threat and contact calls were some parameters associated with high PIC values greater than 2 (PIC values >2.1 ; Figure 4); namely, call duration and the number of units per call.

Discussion

We found that acoustic variability and individual distinctiveness differed across the six main call types of the red-capped man-gabey's vocal repertoire, according to three basic patterns. For loud and alarm calls, which function in long-distance communication, we found low levels of acoustic variability and strong identity coding. In the two food calls, which are usually produced at close range, we found intermediate levels of variability and

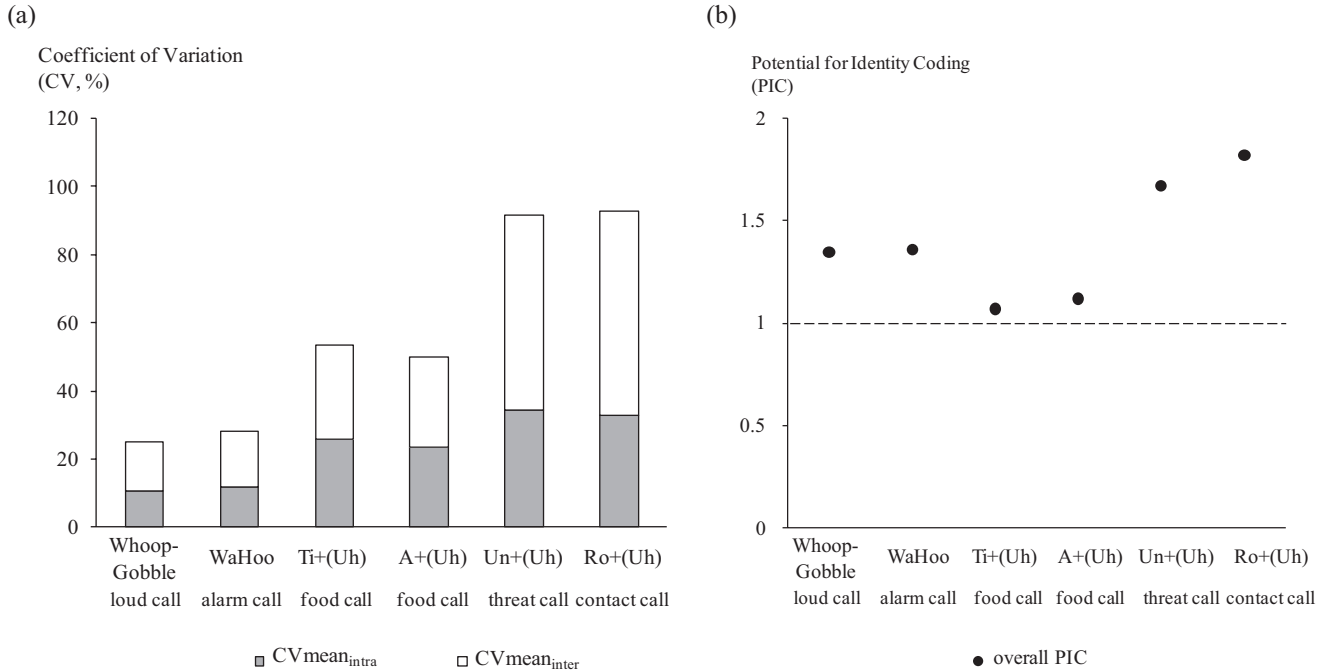


Figure 3. Overall level of (a) intra- and interindividual variability and (b) potential for identity coding of the six call types. (a) Stacked bar chart of CVmean_{intra} and CVmean_{inter}; (b) A PIC value greater than 1 means that this call type can be considered as individual specific.

weak identity coding. Finally, in the threat and contact calls, which function in intragroup social interactions, we found high levels of acoustic variability with strong identity coding. We were able to replicate these basic patterns by analyzing subsamples of the main data set, balanced in terms of individual contribution to carry out dyadic comparisons of the different call types. Since patterns were replicated, we could rule out that they were the result of uneven sample sizes or a biased distribution of individual characteristics, such as age, sex, or body size. Although individually distinctive features were found in every call type, identity coding was not equal across the six call types, but especially strong in calls with a direct within-group social function and, to a lesser degree, long-distance loud and alarm calls. Overall, our results support the *social function* hypothesis in terms of the general acoustic variability across call types, while all three hypotheses are partly supported in what they predicted in terms of individual distinctiveness encoded by calls.

Across call types, frequency parameters were particularly important in enabling individual discrimination. This is perhaps not so surprising as frequency features are known to depend on vocal tract and vocal fold properties, which are correlated to individual characteristics, such as sex, age, and body size (Fitch & Hauser, 1995; Riede, 2010). Identity coding through frequency features has been found in various mammal species (nonhuman primates: Ey et al., 2007; bats: Jones & Ransome, 1993; Campbell's monkeys: Lemasson & Hausberger, 2011; horses: Lemasson et al., 2009). However, individual differences based on temporal features were also observed. They were low in food calls, intermediate in loud and alarm calls, and particularly high in threat and contact calls. Also, the overall level of individual distinctiveness was higher in

alarm, loud, threat, and contact calls compared to the two food calls. The signal duration and the number of units per call are primarily dependent on lung capacity (Fitch & Hauser, 1995), and individuals may have more control over these features compared to frequency parameters. Thus, it appears that red-capped mangabeys generate a higher degree of individual distinctiveness in calls mediating social interactions (i.e., contact and threat calls) in which the temporal parameters play an important role in identity coding.

When investigating acoustic variability and individual distinctiveness across different call types within a species' vocal repertoire, one difficulty lies in the choice of acoustic parameters that can be measured across call types. To carry out comparisons across noisy and tonal structures, consisting of both single and multiple acoustic units, we chose a small set of parameters and focused on the frequency features of the first unit of the call only. In the future, it might be interesting to further investigate, for example, the relative importance of the different units within a call (in case of multiples) with additional measurements.

There are no generally accepted guidelines for choosing acoustic parameters. Variation in frequency patterns and the organizational structure are known to be meaningful to receivers in many mammal species, suggesting that they should be included (fur seals: Charrier, Mathevon, & Jouventin, 2003b; gibbons: Clarke, Reichard, & Zuberbühler, 2006; baboons: Fischer, Cheney, & Seyfarth, 2000; penguins: Jouventin & Aubin, 2002). The ability to discriminate between individuals (or classes of individuals) from their calls alone has also been widely demonstrated in primates, including close relatives of mangabeys (macaques: Hammer-schmidt & Fischer, 1998 and Rendall et al., 1996; baboons: Le-

Table 3
Individual Distinctiveness in the Six Call Types

Call type, Function	PC	% of variance	Eigenvalue	Principal Component Analysis							Analyses of Variance							
				Dcall	#units	Dunit	Factor loading			Fpeak3	Fpeak2	Fpeak1	Wilk's λ	F	df1,df2	P value	# pairs	total of # pairs
							Fbase	Fpeak1	Fpeak2									
Whoop-Gobble, loud call	I	34%	3.42	0.813	0.914	0.651	0.950	0.974	0.619			5.992	10,77	<0.001	60%	90% (9/10)		
	II	31%	1.30								6.405	10,77	<0.001	40%				
	III	19%	1.19						0.926		3.166	10,77	0.002	50%				
WaHoo, alarm call	I	34%	2.95	0.903		0.944			-0.896	0.778	13.858	7,67	<0.001	64.3%	82.1% (23/28)			
	II	26%	1.16								1.654	7,67	0.136	7.1%				
	III	23%	0.86				0.906	0.695			5.822	7,67	<0.001	53.6%				
Ti+(Uh), food call	I	26%	1.90	0.956	0.936		0.828	0.536	0.716		2.744	5,54	0.028	20%	46.7% (7/15)			
	II	23%	1.62			0.570			0.823		4.262	5,54	0.002	40%				
	III	17%	1.10							0.516	2.600	15,144	0.002	0%				
A+(Uh), food call	I	29%	2.187	0.783	0.931	-0.689	0.875	0.737	0.738	-0.855	2.966	8,67	0.007	22.2%	66.7% (24/36)			
	II	24%	1.67								10.212	8,67	<0.001	66.7%				
	III	19%	1.13								0.612	8,67	0.764	0%				
Un+(Uh), threat call	I	31%	2.77	0.917	0.945		0.599	0.672	0.784		4.143	24,189	<0.001	49.1%	74.6% (41/55)			
	II	26%	1.64			-0.547					5.992	10,77	<0.001	43.6%				
	III	19%	0.87				0.615		0.866		3.166	10,77	0.002	25.5%				
Ro+(Uh), contact call	I	34%	2.68	0.954	0.954	0.547	0.762	0.699	0.775	0.937	5.922	30,221	<0.001	57.1%	91.2% (83/91)			
	II	25%	1.42								10.573	13,120	<0.001	52.7%				
	III	16%	1.11								7.877	13,120	<0.001	38.5%				
		MANOVA									8.416	39,350	<0.001					

Note. Left-hand side: Results of the principal component analysis (with Varimax rotation) performed for each call type. For each Principal Component (PC): percentage of variance explained (% of variance), initial Eigenvalue (Eigenvalue), and related acoustic parameters with their factor loadings (NB: only variables with factor loadings >|0.5| had been considered as explanatory). Right-hand side: Results of the analyses of variance tests performed on Principal Components scores, using *caller identity* as fixed factor. For each Principal Component: F statistic (F), between (df1) and within-group (df2) degrees of freedom, P value (P value), proportion of significantly different pairs of individuals out of all possible pairs assessed from post hoc pairwise comparisons LSD tests (# pairs), and proportion of pairs of individuals significantly differing on at least one out of the three Principal Components (total of # pairs).

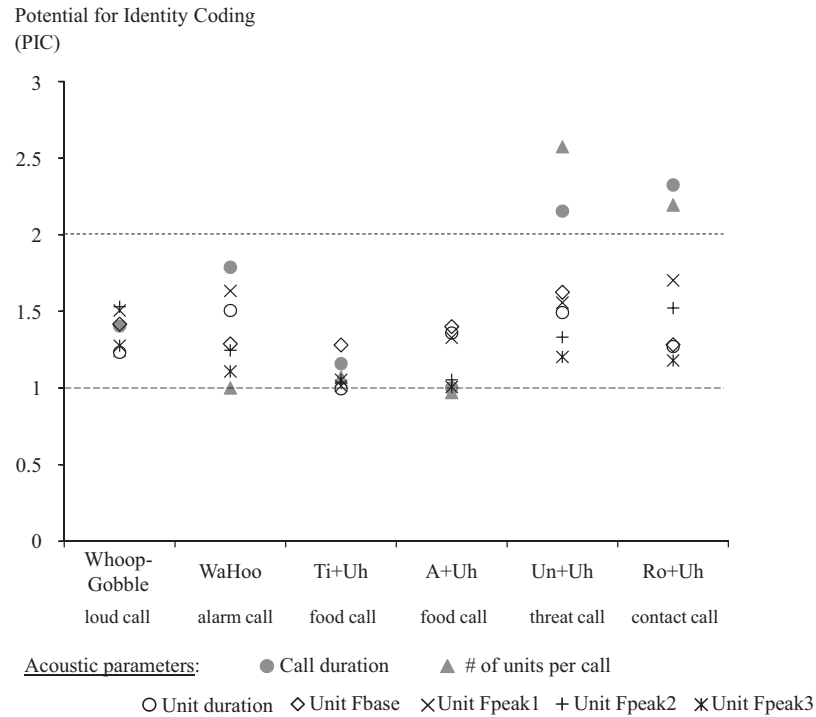


Figure 4. Potential for identity coding of each acoustic parameter for the six call types. A PIC value greater than 1 means that this parameter may be used for individual recognition. PIC values are considered particularly high when greater than 2 (Robisson et al., 1993).

masson, Palombit, & Jubin, 2008 and Semple, 2001), as well as in various other animal species (penguins: Jouventin & Aubin, 2002; horses: Lemasson et al., 2009; elephants: McComb et al., 2003). Eventually, playback experiments will be required to determine whether or not the acoustic variability reported in this study is biologically significant to listeners. Furthermore, a study on the ability of gray-cheeked mangabeys to match a call of a conspecific to its picture revealed that subjects were capable of individual recognition when hearing calls only (namely contact, threat, and alarm calls), as they consequently adjusted their gazing behavior toward pictures (Bovet & Deputte, 2009). Such results in a closely related species suggest that individual acoustic distinctiveness in red-capped mangabeys is perceived by individuals.

A neglected area of research concerns the acoustic variation within the various call types of a species' repertoire. Acoustic variation at the individual call level is important to convey caller identity and details about the event. Three nonexclusive hypotheses have been proposed to explain the sources of such acoustic variation, which relate to our findings in the following way.

In accordance with the *social function* hypothesis, we found that calls with a strong intragroup social function—that is, the contact and threat calls—had high levels of acoustic variability, potentially allowing callers to convey a range of context-specific information. These were calls used in affiliative and agonistic intragroup interactions with a specific social partner. Conversely, the lowest level of variability was observed in the alarm and loud calls, which are produced in response to disturbances to benefit the entire social group or a neighboring group. Intermediate levels of variability were found in the two food calls, which act at the

intragroup level but whose targets are usually not specific. Thus, calls mediating social interactions have a higher potential for encoding socially meaningful acoustic flexibility, potentially allowing callers to adjust their calls according to the social context (quality of the interaction: e.g., macaques: Gouzoules, Gouzoules, & Marler, 1984; Gouzoules & Gouzoules, 1989—identity of the receiver: e.g., pygmy marmosets: Elowson & Snowdon, 1994; macaques: Sugiura, 1998—social bond with the receiver: e.g., squirrel monkeys: Biben, Symmes, & Masataka, 1986—behavior of the receiver: e.g., Japanese macaques: Koda, 2004).

How to best characterize the underlying psychological mechanisms responsible for the observed acoustic variability is part of an ongoing debate (e.g., Seyfarth, et al., 2010). One approach has been to abstain from introducing psychological variables, for example, by describing social calls as plastic structures that encode variables, such as social affinities (Lemasson & Hausberger, 2004). Others have argued that acoustic variability is driven by variability in underlying emotional states, which may be higher in social than nonsocial conditions. According to this line of argument, loud and alarm calls are driven by low variability in arousal, followed by food calls with higher degrees of variation. Social calls, finally, may be most variable due to differential impact by numerous social factors, such as partner identity, interaction intensity, spatial proximity, or behaviors received. Emotion and/or arousal have always been nebulous concepts with little direct heuristic value, but the more general point is that differences in acoustic variation across call types could be driven by how much variation individuals experience when perceiving the event.

An important finding in our study was that the degree of individual distinctiveness of a call type did not correlate with its general acoustic variability. Here, our results were in accordance with the *social function* hypothesis (Charrier et al., 2001), which states that calls that have a relevant social function (i.e., contact and threat calls) should be particularly strong in identity coding. However, calls not used in direct social interactions—that is, alarm and loud calls—also displayed a high degree of individual distinctiveness, a finding not explained by the *social function* hypothesis, but more in line with the predictions of the *distance communication* hypothesis. Both loud and alarm calls (which are also adapted for long-distance communication in this species: Fischer, Hammerschmidt, Cheney, et al., 2002; Waser, 1982) provided stronger identity cues (i.e., showed higher intraindividual stereotypy and individual distinctiveness) than the two food calls used during short-distance social interactions. More generally, our results show that there is no intrinsic relation or trade-off between interindividual and intraindividual acoustic variation. Instead, we observed that both highly stereotyped and highly variable calls could display high degrees of individual acoustic distinctiveness.

Lastly, our results only partially follow the predictions of the *structure-affective processing* hypothesis. One of its features is that calls that function in altering attention, arousal, and affect in listeners—that is, loud, alarm, and food calls in our case—should have acoustic features that alter listeners' behavior directly; for example, through sharp onsets, high-amplitude noisiness, repeated energy pulses, or frequency and amplitude fluctuations. These acoustic features are said to prevent individual distinctiveness (Owren & Rendall, 1997, 2001), something that we found in food calls but not alarm or loud calls. The contact and threat calls, on the other hand, both had a tonal acoustic structure well suited for identity coding (Owren & Rendall, 1997, 2001) and accordingly, we found a high degree of individual distinctiveness. A second feature of the *structure-affective processing* hypothesis is the idea that some acoustic features function better in conditioning processes, an idea put forward by Guilford and Dawkins (1991) and further developed by Owren & Rendall (1997, 2001). We did not test for differences in the learnability of the different calls but the presence of individual acoustic cues in calls used in short-range communication is in line with this general proposal. Callers may benefit if receivers learn quickly to associate individual voice cues in social calls with positive (e.g., grooming or approach for contact calls) or negative outcome (e.g., biting or chasing for threat calls). Experimental work would be required to test this idea more thoroughly.

In sum, our study provided evidence that acoustic variability and individual distinctiveness was not homogeneously distributed across the main call types of this species. There is an interesting parallel in human speech with regards to the relationship between the context of communication and individual distinctiveness. Both the number of targeted receivers (mass communication vs. one-on-one conversation) and the composition of the audience (strangers vs. familiar individuals) have significant effects on the amount of individual distinctiveness present in human vocal behavior (reviewed in Bell, 1984).

The high degree of individual distinctiveness and high level of acoustic variability in the two calls used in direct social interactions (i.e., threat and contact calls) highlight the possible role of social factors on the evolution of the vocal repertoire in primates,

in line with previous similar findings in Campbell's monkeys (Lemasson & Hausberger, 2011). The need for individual recognition and behavioral flexibility during direct social interactions seems to have exerted a selective pressure on the acoustic morphology of the associated calls. In this regard, our study supports the general theory of a social-vocal coevolution of communicative abilities (Lemasson, 2011), suggesting that social pressures have played a key role in the evolution of vocal plasticity, including human speech. Further empirical studies (such as studies in different species with functionally similar but structurally dissimilar call types, or in different species with different social systems) are needed to explore the relation between acoustic variability, individual distinctiveness, and call function. As such, our study may open new avenues of comparative research in nonhuman primates with the ultimate goal of understanding how human speech and language has evolved.

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