



# Tolerant and intolerant macaques differ in the context specificity of their calls and how they ‘comment’ on the interactions of others

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## Abstract

The ‘social complexity hypothesis for communicative complexity’ posits that living in a complex social system requires complex communication skills. Since the complexity of a system can be measured by the amount of uncertainty it produces, we tested this hypothesis by studying species of macaque that differ in social tolerance and uncertainty of social interactions. We studied vocal communication in groups of macaques belonging to four species: Japanese and rhesus macaques, which are characterized by low levels of social tolerance and low uncertainty in the outcome of social interactions, and Tonkean and crested macaques, which display high levels of tolerance and uncertainty in interactions. We recorded the vocalizations emitted by adult females in agonistic, affiliative and neutral contexts. We measured call duration, entropy and time and frequency energy quantiles and processed these variables using cluster analyses and permutational multivariate analyses of variance. We found that tolerant macaques had a weaker relationship between the acoustic structure of calls and their context of emission compared to intolerant macaques. The study of ‘commenting calls’, i.e. calls made by individuals attending interactions between groupmates, also showed that their acoustic structure was more differentiated from other calls in tolerant Tonkean and crested macaques than in intolerant rhesus macaques. The flexibility of vocal production therefore appears to be correlated with the level of uncertainty of social interactions. Species with more complex social interactions were also those with higher degree of freedom in the association between acoustic structure and social context, which supports the social complexity hypothesis.

## Significance statement

Is there a relationship between the complexity of social systems and the complexity of communication skills? Animals living in complex social environments are expected to use a wide variety of messages related to different goals and contexts. The complexity of a system can be assessed by the amount of uncertainty it can produce. We investigated the complexity of vocal communication by comparing two species of macaque displaying low uncertainty in their social interactions, with two other macaque species displaying high levels of uncertainty in their interactions. The comparison showed that call flexibility was related to uncertainty levels. Species with higher levels of uncertainty had weaker associations between acoustic structure and social context. These results support the hypothesis of a link between social system complexity and communication complexity, which has important implications for our understanding of the evolution of social and communication systems.

**Keywords** Social complexity · Uncertainty · Flexibility · Communication · Acoustics · Primates

## Introduction

Living in a complex social system means interacting with different social partners in varied situations. This social complexity requires sophisticated communicative skills so that individuals can express a wide range of intentions and emotional states. This is what the ‘social complexity

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hypothesis for communicative complexity' posits, which has become a topical issue in recent years (Freeberg et al. 2012; Peckre et al. 2019; Pollard and Blumstein 2012; Roberts and Roberts 2020). However, as discussed elsewhere, a recurring problem is how to define and measure complexity (Rebout et al. 2021). The preferred measures of social complexity are the number of individuals in a social group (Freeberg 2006; Lehmann and Dunbar 2009; Dunbar 2012; Bergman and Beehner 2015) and also the different types of group members (Blumstein and Armitage 1997; Pollard and Blumstein 2012). However, these measures are rather crude proxies that do not consider how individuals interact (Shultz and Dunbar 2006). It has therefore been proposed to use the number of social interactions (Freeberg et al. 2012) or the number of social relationships instead (Bergman and Beehner 2015; Fischer et al. 2017a, b; Morrison et al. 2020). Such indices are valuable because they reflect social diversity, but diversity alone cannot yet sum up the entire complexity of social systems (Rebout et al. 2021).

With regard to vocal complexity, the variable most often considered is the number of units in a communicative system and in particular the number of vocalizations in a species repertoire (Freeberg et al. 2012; Pollard and Blumstein 2012; Schamberg et al. 2018; Peckre et al. 2019). Another measure is the amount of information in a vocal repertoire, calculated as the number of bits of information using Shannon's uncertainty formula (Shannon 1948; Freeberg 2006; Bouchet et al. 2013). These two variables only concern vocal diversity. In addition, they are difficult to implement in animals with a graded repertoire, that is, a continuum of acoustic structures without clear boundaries between different types of calls (Hammerschmidt and Fischer 1998; Wadewitz et al. 2015). For this reason, it has been recommended to assess vocal complexity by quantifying the degree of gradation of the vocal repertoire (Wadewitz et al. 2015; Fischer et al. 2017a, b) and thus the flexibility of acoustic structures in a species (Rebout et al. 2020). Flexibility can also manifest itself in the extent of context specificity of vocal signals, i.e. the degree of freedom between their acoustic structure and the context in which they are emitted (Wheeler and Fischer 2012). Note that in statistics the degree of freedom corresponds to the number of variables that cannot be fixed by an equation; here the equation is the context, and the variables are the types of calls that can be emitted. This means that the more calls are 'fixed' by the context, the less uncertainty there is in the system. On the contrary, when the calls are little 'fixed' by the context, the system has a higher level of uncertainty.

In animal communication, the question of the relationship between structure and function is not a simple one. Many vocal signals are not context-specific, and acoustically similar calls can occur in different social situations, while acoustically dissimilar calls can be emitted in the same social situations; this has led to the idea that the structure of

signals has no special relationship with their social function (see Owren and Rendall 2001). On the other hand, the motivation-structural rules proposed by Morton (1977) assume that there is a relationship between the physical structure of sounds and the motivations behind them. Some sounds may be more likely than others to induce attention, arousal or emotional responses in conspecifics, and call structure may then be partially predicted from the context. In mammals, for instance, calls produced in affiliative contexts tend to be associated with lower amplitude and variability, higher frequency modulation and less noisy signals than agonistic and alarm-related contexts (Morton 1977; Owren and Rendall 2001; Lemasson and Hausberger 2011; Briefer 2012; Bouchet et al. 2013; Gustison and Townsend 2015; Mercier et al. 2019). Flexibility in the degree of correspondence between vocal signals and their context of occurrence contributes to the complexity of communication systems (Manser et al. 2014; Pika 2017; Peckre et al. 2019).

Although there is no consensus on a general definition of complexity, there is agreement that the behaviour of complex systems is difficult to predict (McDaniel and Driebe 2005; Schuster 2016). We have therefore proposed that it is possible to assess the complexity of systems based on their ability to produce uncertainty (Rebout et al. 2021). When studying communicative complexity, we can rely on the degrees of freedom in the association between signals and their context of emission to quantify uncertainty. For instance, a strong connection between a vocal signal and a given context implies a low degree of uncertainty in the system: when hearing a highly context-specific call, the listener does not need information about the context to identify the information encoded by the acoustic structure of the call; by contrast, when a call has low context specificity, uncertainty about the message is greater and the listener needs additional contextual cues to respond appropriately (Seyfarth and Cheney 2003; Wheeler and Fischer 2012; Manser et al. 2014).

While the strength of the association between the structure of a vocal signal and the context in which the caller is involved is variable, there is an additional level of complexity when calls are triggered by a social context in which callers are not themselves involved. Such a situation has been reported in Barbary macaques (*Macaca sylvanus*) where a bystander may vocalize while attending an interaction between group mates (Brumm et al. 2005). The bystander is not involved in the social interaction and shows no other response than to vocalize, which is why Brumm and collaborators (Brumm et al. 2005) described these calls as 'comments'. They suggest that the comments draw the attention of others to the event, but that they could also include an evaluation of the event (Brumm et al. 2005). It is not known whether commenting calls have a specific acoustic structure. If they were to differ from calls emitted by individuals in the

absence of any interaction—i.e. neutral calls—such flexibility would make the communication system more complex by providing individuals with a greater number of expressive options.

In an earlier study, we have found interspecific contrasts in the diversity and flexibility of the structure of vocal signals in four species of macaque. While phylogenetic relationships between species failed to account for these results, the social complexity hypothesis for communicative complexity successfully explained them (Rebout et al. 2020). In this study, we compared the four species by analysing separately three social contexts (agonistic, affiliative, neutral) in which vocalizations were emitted. This revealed species differences in the number of call categories and the degree of gradation between these categories. However, a comparison of vocalizations occurring in different social contexts remains to be made to determine whether the degree of specificity of call structure to social context can be related to the degree of uncertainty in species-typical social style.

Here, we extend the comparative study of flexibility by comparing the structure of calls occurring in different contexts to investigate the strength of the association between vocal structure and social context. Macaque species are well suited for this purpose. Macaques are semi-terrestrial primates. They live in groups that include both adult males and adult females. Males disperse and females remain in their natal group where they constitute matriline, i.e. subgroups of individuals related by maternal descent (Thierry 2007). Although they share the same patterns of organization, macaques show a wide range of variation regarding their degree of social tolerance, which is associated with varying levels of uncertainty about the outcome of agonistic interactions (Dobson 2012; Zannella et al. 2017). In the more intolerant species, social conflicts have unequivocal effects: in Japanese macaques (*Macaca fuscata*) and rhesus macaques (*M. mulatta*), for example, the receiver of the aggression submits or flees in nine out of ten cases in unrelated females (Thierry et al. 2008). By contrast, in the more tolerant species, the receiver of the aggression often protests or counter-attacks: in Tonkean macaques (*M. tonkeana*) and crested macaques (*M. nigra*), 68.0% and 45.4% of conflicts in unrelated females, respectively, remain undecided, without clear winner or loser (Thierry et al. 2008). The interspecific variations found in the agonistic patterns of macaques correlate with the other components of their social styles. Tolerant macaques reconcile more frequently and have a greater number of facial displays than their more intolerant counterparts, they perform better in experimental tasks requiring individuals to display inhibitory control or pointing gestures and their social behaviours are less constrained by kinship and dominance relationships than those of intolerant macaques; as a corollary, the outcomes of their social interactions are less predictable than those of intolerant

macaques (Thierry 2007; Dobson 2012; Joly et al. 2017; Balasubramaniam et al. 2018).

We compared two tolerant species (Tonkean and crested macaques) with two intolerant species (Japanese and rhesus macaques). They are mainly frugivorous, and their primary habitat is forest, but rhesus macaques can live in various habitats, from forests to dry lands and regions of human settlement (Ménard 2004). Their repertoire of vocalizations is graded (Rowell and Hinde 1962; Green 1975; Masataka and Thierry 1993; Gouzoules and Gouzoules 2000; Panggur 2013). Based on the social complexity hypothesis for communicative complexity, it can be assumed that the degree of flexibility of a communicative system is related to the degree of uncertainty of social interactions and relationships. Using this reasoning, we expect that ambiguous social situations create a need for greater call flexibility, allowing more information to be conveyed. This can apply both to individuals involved in social interactions and to third parties who comment on these interactions. We examined the structure of the vocal signals produced in three social contexts (agonistic, affiliative and neutral) to test the two following predictions: (1) *Context specificity of calls*: analysis of the structure of calls according to their contexts of emission should reveal that a given acoustic structure may occur in more contexts in tolerant macaques than in intolerant macaques, pointing to a weaker relationship between call structure and social context in the former. (2) *Form of commenting calls*: by conveying information about ongoing social events, comments have the potential to decrease any uncertainty individuals may have about their social environment; analysis of the structure of comments made by bystanders should reveal that their degree of differentiation from contact calls emitted in the absence of any interaction is more pronounced in tolerant than in intolerant macaques, pointing to a weaker relationship between call structure and bystander context in the former. It should be added that measuring the strength of the association between social context and vocal structure is a methodological challenge in species with a graded repertoire of vocalizations. We had to develop specific methods using clustering algorithms and Shannon's information theory to test these predictions.

## Methods

### Subjects and conditions

We made acoustic recordings and behavioural observations of adult females: 13 females in four groups of Tonkean macaques, 51 females in two groups of crested macaques, 29 females in two groups of Japanese macaques and 16 females in two groups of rhesus macaques. We focused on adult females as their age and sex category are the most

represented in macaque groups and also because they contribute the most to vocal activity (Lemasson et al. 2013). Japanese, rhesus, and Tonkean macaque females were born in captivity and were at least five years old. We studied crested macaques in the wild, assessing their age from their reproductive history since 2006 (Macaca Nigra Project), body size, nipple shape and the presence of scars. The composition of groups is presented in Table 1.

Groups of Japanese macaques (Ft, Fw) were kept in two enclosures of 960 and 4600 m<sup>2</sup> at the Primate Research Institute in Inuyama, Japan (Arlet et al. 2015). Groups of rhesus macaques (Ma, Mb) were kept in two 210-m<sup>2</sup> enclosures at the Biomedical Primate Research Center in Rijswijk, Netherlands (De Marco et al. 2019). One group of Tonkean macaques (Tb) was kept in a 120-m<sup>2</sup> enclosure at the Orangerie Zoo in Strasbourg, France, and the other three groups (Tc, Td, Te) were kept in 500-m<sup>2</sup> enclosures at the rescue centre Parco Faunistico di Piano dell'Abatino in Rieti, Italy (De Marco et al. 2019). Enclosures were wooded or furnished with ropes, poles and shelters. Animals were fed with

commercial pellets, complemented with vegetables and fresh fruits. Water was available ad libitum. Groups of crested macaques (Npb, Nr1) lived in the Tangkoko Nature Reserve, Sulawesi, Indonesia (Micheletta et al. 2013). They inhabit lowland tropical rainforest and were not provisioned (Collins et al. 1991; Rosenbaum et al. 1998).

## Data collection

We made outdoor observations to achieve quality recordings. Observers were within 5 m of the emitters. Data were taken by AL in Japanese macaques (Arlet et al. 2015); NR in rhesus macaques; NR, ADM and AS for Tonkean macaques (De Marco et al. 2019); and JM in crested macaques (Micheletta et al. 2013) (Table 1). It was not possible to record data blind because our study involved focal individuals living in social groups. The subjects were observed in a predefined random order with focal sampling. The sample duration was 10 mn for Japanese macaques and Tonkean macaques in groups Tc, Td and

**Table 1** Information about groups and subjects (Takahashi et al. 2006; Micheletta et al. 2013; Arlet et al. 2015; De Marco et al. 2019)

Groups	Dates of group foundation and study	Composition of groups	Name and age in years of females <sup>1</sup>
Rhesus macaque group Ma	founded in 2004, studied in Jul–Oct 2016	10 adult females, 3 adult males, 22 immatures <sup>2</sup>	<i>Pip</i> (14), <i>But</i> (13), <i>Isa</i> (11), <i>Nil</i> (10), <i>Hoe</i> (10), <i>Wie</i> (9), <i>Lok</i> (7), <i>Aus</i> (6), <i>Mon</i> (5), <i>Pan</i> (5)
Rhesus macaque group Mb	founded in 2004, studied in Jul–Oct 2016	6 adult females, 1 adult male, 24 immatures	<i>Tro</i> (13), <i>Plo</i> (12), <i>Hat</i> (10), <i>Jah</i> (8), <i>Kwe</i> (7), <i>Ymi</i> (6)
Tonkean macaque group Tb	founded in 1978, studied in Feb–May 2016	4 adult females, 6 adult males, 5 immatures	<i>Gil</i> (27), <i>Gai</i> (9), <i>Giu</i> (9), <i>Lis</i> (5)
Tonkean macaque group Tc	founded in 2005, studied in Sept–Dec 2014	4 adult females, 4 adult males, 8 immatures	<i>Pal</i> (13), <i>Sop</i> (11), <i>Pam</i> (8), <i>Pap</i> (6)
Tonkean macaque group Td	founded in 2007, studied in Mar–May 2015	3 adult females, 5 adult males, 7 immatures	<i>Sib</i> (12), <i>Tet</i> (11), <i>Tan</i> (11)
Tonkean macaque group Te	founded in 2009, studied in Sept–Dec 2014	2 adult females, 3 adult males, 5 immatures	<i>Nin</i> (15), <i>Nif</i> (9)
Japanese macaque group Fw	founded in 1974, studied in Mar–Aug 2005	13 adult females, 4 adult males, 10 immatures	<i>Has</i> (10), <i>Min</i> (6), <i>Mia</i> (5), <i>Nir</i> (6), <i>Rek</i> (14), <i>Rum</i> (17), <i>Mil</i> (9), <i>Bel</i> (5), <i>Lar</i> (5), <i>Som</i> (18), <i>Sar</i> (8), <i>Jes</i> (7), <i>Ren</i> (20)
Japanese macaque group Ft	founded in 1970/1971, studied in Mar–Jul 2005	16 adult females, 6 adult males, 24 immatures	<i>Ame</i> (25), <i>Iwa</i> (11), <i>Kak</i> (8), <i>Kin</i> (15), <i>Kam</i> (5), <i>Kur</i> (9), <i>Mor</i> (22), <i>Shi</i> (10), <i>Sha</i> (8), <i>Tan</i> (24), <i>Tak</i> (17), <i>Tsu</i> (21), <i>Umi</i> (19), <i>Ume</i> (8), <i>Yam</i> (13), <i>Yuk</i> (21)
Crested macaque group Nr1	wild population, studied between Sept 2010 & Feb 2011	28 identifiable adult females	<i>Ani</i> , <i>Adi</i> , <i>Bea</i> , <i>Bas</i> , <i>Cin</i> , <i>Dor</i> , <i>Ern</i> , <i>Fen</i> , <i>Glo</i> , <i>Hel</i> , <i>Isa</i> , <i>Jos</i> , <i>Kat</i> , <i>Leo</i> , <i>Min</i> , <i>Nur</i> , <i>Oli</i> , <i>Pol</i> , <i>Qut</i> , <i>Ros</i> , <i>Sup</i> , <i>Tut</i> , <i>Eli</i> , <i>Vod</i> , <i>Wi</i> , <i>Big</i> , <i>Yan</i> , <i>Zoe</i>
Crested macaque group Npb	wild population, studied between Sept 2010 & Feb 2011	23 identifiable adult females	<i>Agn</i> , <i>Bia</i> , <i>Cic</i> , <i>Dea</i> , <i>Eva</i> , <i>Fio</i> , <i>Geu</i> , <i>Her</i> , <i>Iye</i> , <i>Jan</i> , <i>Kri</i> , <i>Lid</i> , <i>Nao</i> , <i>Oma</i> , <i>Ram</i> , <i>Ste</i> , <i>Jam</i> , <i>Mal</i> , <i>Zor</i> , <i>Pap</i> , <i>Val</i> , <i>Tem</i> , <i>Upi</i>

<sup>1</sup>Age at the beginning of data collection. The names of the sampled females are in italics

<sup>2</sup>Individuals less than 5 years of age

Te; 15 mn for rhesus macaques and Tonkean macaques in group Tb; and 30 mn for crested macaques. This gave  $6.1 \pm 0.16$  h (mean  $\pm$  SD) of focal sampling per female for Japanese macaques,  $12.7 \pm 0.7$  h for rhesus macaques,  $13.6 \pm 3.2$  h for Tonkean macaques and  $7.8 \pm 0.4$  for crested macaques.

For the Japanese macaques, we made vocal recordings using a TCD-D100 Sony (Tokyo, Japan) DAT recorder (WAV format, 44,100-Hz sampling frequency, 16-bit resolution) and an ECM-672 Sony directional microphone. For rhesus and Tonkean macaques, we used a Marantz (Eindhoven, Netherlands) PMD661 recorder (WAV format, 44,100-Hz sampling frequency, 16-bit resolution) and a Sennheiser (Wedermark, Germany) K6/ME66 directional microphone. For the crested macaques, we used partly a high-resolution camera Panasonic (Osaka, Japan) HDC-SD700 connected to a Sennheiser (Wedermark, Germany) K6/ME66 directional microphone. We extracted the audio tracks from the video recordings with the software *FFmpeg* (v 3.4.1) leading to WAV format (sampling frequency: 32 000 Hz, resolution: 16 bits). We collected observational data on the contexts of call emission using a lavalier microphone connected to the recorder in Japanese, rhesus and Tonkean macaques (at805f, Audio-Technica, Leeds, United Kingdom or TCM 160, Meditec, Singapore). For crested macaques, the observer filmed the focal individual while a field assistant recorded contextual data using a handheld computer.

We identified three different social contexts: agonistic, affiliative and neutral. We distinguished these contexts on the basis of the behaviours that could occur in the 3 s before or after the emission of a call or a sequence of calls. We defined a sequence as a series of calls separated by a maximum of 3 s. The behavioural units were based on published repertoires in macaques (Altmann 1962; Fedigan 1976; Thierry et al. 2000). The agonistic context was defined by the occurrence of aggression (facial threat display, supplantation, lunge, chase, slap, grab, bite) and response to aggression (aggression, submissive facial display, crouch, avoidance, flight). The affiliative context was defined by the occurrence of affiliative behaviour (affiliative facial display, approach, grasp, embrace, mount, social play, social grooming, sitting in contact). In the neutral context, the emitter was not involved in a social interaction.

To investigate the degree of differentiation of commenting calls, we distinguished three categories of calls according to the degree of involvement of emitters in social interactions:

*Interaction call*: the emitter is engaged in an agonistic or affiliative interaction in the 3 s before or after the utterance of a call or a sequence of calls.

*Commenting call*: an agonistic or affiliative interaction occurs in the 3 s before the utterance of the call or the

sequence of calls but the emitter is not involved in the interaction.

*Uncontextualized call*: no social interactions occur in the 3 s before or after the emission of a call or a sequence of calls; we have removed from the analysis the calls and sequences of calls where a non-social event (e.g. any event related to human activity) occurred in the 3 s preceding it.

From the point of view of the emitter's calls, both commenting and uncontextualized calls occurred in the neutral context. We could not distinguish these two types of calls in Japanese macaques because the observer did not record social interactions other than those in which the emitter was directly involved. The assessment of the valence of commenting calls (agonistic or affiliative) was based on the types of calls recognized in macaques (Rowell and Hinde 1962; Lindburg 1971; Green 1975; Peters 1983; Lewis 1985; Masataka and Thierry 1993; Pangur 2013). All uncontextualized calls were identified by the human ear as coos or growls.

Recording conditions were not the same in the different species, especially in the wild population of crested macaques relative to the captive groups studied in the other three species. Rather than directly comparing the acoustic structure of the calls in the different species, we studied the strength of the relationship between the structure of the calls and their emission context in each species and then tested whether social contexts produce similar or different effects on the structure of the calls in the four species.

## Acoustic analysis

We sampled 1368 calls in Japanese macaques, 1026 in rhesus macaques, 1210 in Tonkean macaques and 1234 in crested macaques. We visualized spectrograms in the software Raven Pro 1.4 (Center for Conservation Bioacoustics 2011) with a 256 fast Fourier transform length and a Hanning window. We measured eight variables using the same software:

*Duration*: duration in seconds from the beginning to the end of a call

*Q2 time*: duration in seconds dividing a call into two intervals of equal energy

*Q2 ratio*: ratio in percent between Q2 time and duration

*Q1 frequency*: value in hertz of the frequency dividing a call into two intervals containing 25% and 75% of the energy

*Q2 frequency*: value in hertz of the frequency dividing a call into two intervals of equal energy

*Q3 frequency*: value in hertz of the frequency dividing a call into two intervals containing 75% and 25% of the energy

*Wiener's aggregate entropy*: degree of disorder (i.e. noisiness) of the call utilizing the total energy in a frequency bin over the entire call

*Wiener's average entropy*: mean of the mean entropies of the different time slices of a call

We first sorted records according to their quality for these variables. We then randomly selected a maximum of three calls per sequence. Females whose sample size was less than five calls were removed from the analysis. We also excluded some specific types of calls that were not present in the samples of all species (alarm calls) or that had no equivalent in all species (œstrus calls, twits, cackles). Our sample yielded 2469 calls (Table 2). We provide spectrograms of the main types of vocalizations in the four species of macaques in the supplementary material ESM1.

## Statistical analyses

We performed statistical analyses in R (R Core Team 2018). A first analysis focused on the context specificity of calls in order to assess the degree of association between acoustic structures and social contexts. Our goal was to examine the extent to which the classification of calls based on their acoustic structure would correspond to the classification of calls according to social context in each species and thus address the strength of the association between the call structure and their emission context. We developed our own methods to solve the issue. We used a cluster algorithm to group calls in an objective way, i.e. based solely on acoustic structure. Then, we evaluated in these groups of structures the proportion of the different contexts by reasoning that the higher the degree of association between the acoustic structure of the calls and their emission context, the more the groups are each mainly composed of a single emission context. On the contrary, the lower the degree of association between structure and context, the more groups are composed of calls from different contexts.

We designed a 4-step procedure. We first described the calls with seven acoustic variables. To reduce the dimensionality of the dataset and obtain a summary data space with less noise, we applied a Principal Component Analysis (PCA), which allowed us to limit correlations between factors that could influence clustering. Before the PCA, we scaled the acoustic variables to yield a standard deviation of one and a mean of zero with the *R base* function *scale* in each species. The analysis was carried out with the function *PCA* of the package *FactoMineR* (Lê et al. 2008). To balance the contribution of each individual to the creation of the space and give equal weight to each female, we balanced females depending on the number of their calls by using the argument *row.w* of the function *PCA*.

In a second step, we performed a hierarchical cluster analysis using the function *hclust* of the package *FactoMineR* (Lê et al. 2008). We set the number of clusters for each species at 9, based on the mean number of broad categories of calls per context in macaques (Rebout et al. 2020). For this hierarchical cluster analysis, since our dataset contained different numbers of calls for each social context, we randomly sampled 50 calls per context, so each context had the same probability of occurring in any cluster if they were distributed entirely at random. For example, if the sample was biased towards a particular social context, it was more likely that the clusters were composed of this social context.

In a third step, we measured the extent to which the same acoustically based cluster of calls could be emitted in different social contexts. To compare proportion of contexts in relation to uncertainty, we applied information theory to calculate an uncertainty value for each of the 9 clusters, based on the formula of Shannon (1948):

$$H = - \sum_{i=1}^S p_i \log p_i$$

$h$  is the Shannon's uncertainty,  $S$  is the number of social contexts and  $p_i$  is the proportion of calls in the cluster for the context  $i$ .  $H$  varies from near zero (one social context is highly predominant in the cluster) to a maximum value of

**Table 2** Total number of calls and mean number ( $\pm$ SD) of calls processed in each species

Species (number of subjects)	Agonistic context		Affiliative context		Neutral context	
	Total number	Mean number $\pm$ SD	Total number	Mean number $\pm$ SD	Total number	Mean number $\pm$ SD
Japanese macaque ( $N=24$ )	79	3.30 $\pm$ 3.77	94	3.92 $\pm$ 4.16	255	10.6 $\pm$ 5.48
rhesus macaque ( $N=16$ )	118	7.38 $\pm$ 6.75	59	3.69 $\pm$ 3.22	461 <sup>1</sup>	28.8 $\pm$ 16.0
Tonkean macaque ( $N=13$ )	270	20.8 $\pm$ 26.3	226	17.4 $\pm$ 14.3	202 <sup>2</sup>	15.5 $\pm$ 8.42
crested macaque ( $N=19$ )	201	10.6 $\pm$ 6.61	297	15.6 $\pm$ 11.8	191 <sup>3</sup>	10.1 $\pm$ 7.40

<sup>1</sup>Including 31 comments and 265 uncontextualized calls, <sup>2</sup>Including 36 comments and 115 uncontextualized calls, <sup>3</sup>Including 39 comments and 122 uncontextualized calls

$\log S$  (the cluster is composed of the three social contexts in the same proportions).

For comparative purposes, we used the relative index (Pielou 1969; Peet 1974):

$$h = \frac{H}{H_{max}}$$

$H_{max}$  is the maximal value of  $H$ , i.e.  $\log S$ .

This value quantitatively expresses the uncertainty in identifying the context associated with a particular signal structure. If there is a strict relationship between the structure of calls and their social context, then each cluster should contain mainly calls belonging to a single context (i.e. low uncertainty). On the contrary, if the relationship between acoustic structure and social context is looser, the proportions of calls belonging to different contexts within each cluster should be more even (i.e. high uncertainty). We then transformed the uncertainty values of each cluster into relative uncertainty values: the uncertainty was divided by the logarithm of the number of categories, i.e. the number of social contexts. The relative uncertainty value closes in on 0 as the cluster approaches a state where it only contains calls from the same social context. The relative uncertainty value closes in on a maximum—the log of 3—when the cluster approaches a state where it contains as many calls from each social context. We finally calculated the mean from the relative index of the nine clusters. See the supplementary material ESM1 for more information.

Lastly, we statistically compared the mean relative uncertainty values of the four species of macaque. We repeated the sampling procedure, clustering procedure, and uncertainty analysis using bootstraps, with a number of 30 repetitions per species. We set the number of repetitions at 30 based on the central limit theorem. This allowed us to have enough data to be able to make meaningful statistics, but not so much as to push the power of the test, which could lead to significant but subtle differences. This resulted in four mean relative uncertainty values, one for each species, based on 30 random samples. We compared the relative uncertainty values between species using a linear model (LM). We compared the complete model (i.e. the one with the species) to the null model (i.e. the one without the species) with likelihood ratio tests (LRT) using the function *lrtest* of the package *lmtree* (Zeileis and Hothorn 2002). This made it possible to test whether the species factor had an effect. Finally, we used post hoc tests to make paired comparisons of species using the function *emmeans* of the package *emmeans* (Lenth et al. 2018).

We conducted a second analysis to examine the form of the commenting calls. Here, the goal was no longer to study whether a given acoustic structure belongs preferentially to one context, so we needed a specific statistical approach to

test whether an individual involved in one context can vocally refer to another context. We tested the existence of acoustic differences between interaction, commenting and uncontextualized calls in rhesus, Tonkean and crested macaques. To quantify the possible differences between species in terms of acoustic variables, hereafter referred to as *acoustic distance*, we used Permutational multivariate analysis of variance (PERMANOVA) to test whether the centroids (mean) of the three categories of calls were statistically equivalent in the multidimensional space. We used the function *adonis* from the package *vegan* (Oksanen et al. 2019). Since PERMANOVA assumes no distribution, its usage fits our dataset, and its insensitivity to multiple correlations allowed us to keep all acoustic parameters. We ran *adonis* using Euclidean distances—as the logical choice to represent acoustic distances—and ran 1000 permutations, as advised by Oksanen and collaborators (2019). In order to take into account the pseudoreplication of each macaque individual, we limited the permutations using the argument *strata* based on individual identity in the *adonis* function. For paired comparisons between contexts, we applied the function *pairwise.adonis* of the package *pairwiseAdonis* (Arbizu 2017), using the same *strata* specification to constrain permutations. The data were represented using PCA of the packages *FactoMineR* and *factoextra*, with 95% confidence ellipses.

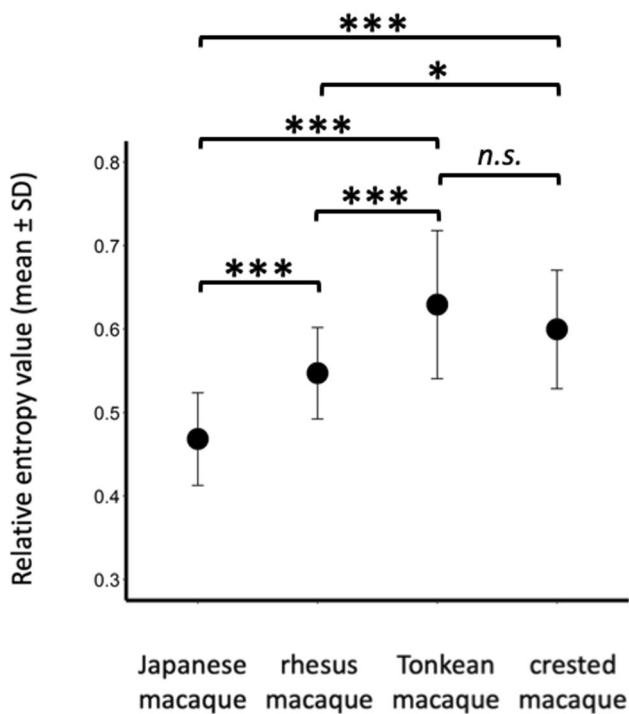
## Results

### Context specificity of calls

The degree of context specificity of calls, as measured by relative uncertainty values, differed between species (LRT  $\chi^2=71.4$ ,  $p<0.001$ ) (Fig. 1). Post hoc tests revealed that the relative uncertainty values of Tonkean macaques and crested macaques did not differ significantly (estimate  $\pm$  SE =  $-0.030 \pm 0.018$ ,  $t=1.67$ ,  $p=0.344$ ). Japanese macaques had a significantly lower value compared to rhesus (estimate =  $-0.079 \pm 0.018$ ,  $t=-4.44$ ,  $p<0.001$ ), Tonkean (estimate =  $-0.161 \pm 0.018$ ,  $t=-9.05$ ,  $p<0.001$ ) and crested macaques (estimate =  $-0.131 \pm 0.018$ ,  $t=-7.38$ ,  $p<0.001$ ). Rhesus macaques had a significantly lower value than Tonkean (estimate =  $-0.082 \pm 0.018$ ,  $t=-4.61$ ,  $p<0.001$ ) and crested macaques (estimate =  $-0.052 \pm 0.018$ ,  $t=-2.94$ ,  $p=0.020$ ).

### Form of commenting calls

The degree of differentiation of commenting calls differed according to species. In rhesus macaques, the multivariate acoustic distance was not significantly different from zero between commenting and uncontextualized calls,



**Fig. 1** Degree of association between acoustic structure and social context as measured by relative uncertainty values in the four species of macaque (\* $p < 0.05$ , \*\*\* $p < 0.001$ )

which means that they did not differ significantly according to their acoustic variables (pseudo- $F = 3.46$ ,  $p = 0.110$ ). However, the distance was significantly different from zero between interaction and commenting calls (pseudo- $F = 3.70$ ,  $p < 0.001$ ) and between interaction and uncontextualized calls (pseudo- $F = 41.3$ ,  $p < 0.001$ ), which means that interaction calls differed significantly from commenting and uncontextualized calls according to their acoustic variables (Fig. 2). In Tonkean macaques, the three acoustic distances were significantly different from zero (interaction vs. commenting calls: pseudo- $F = 10.8$ ,  $p < 0.001$ ; commenting vs. uncontextualized calls: pseudo- $F = 57.5$ ,  $p < 0.001$ ; interaction vs. uncontextualized calls: pseudo- $F = 6.08$ ,  $p < 0.001$ ) (Fig. 2). In crested macaques, the acoustic distance was noticeable but not significantly different from zero between interaction and commenting calls, which means that they did not significantly differ (pseudo- $F = 1.82$ ,  $p = 0.493$ ). However, the acoustic distance was significantly different from zero between commenting and uncontextualized calls (pseudo- $F = 13.4$ ,  $p < 0.001$ ) and between interaction and uncontextualized calls (pseudo- $F = 27.5$ ,  $p < 0.001$ ), which means that uncontextualized calls differed significantly from commenting calls and interaction calls (Fig. 2). Lastly, the context of a proportion of commenting calls ( $N = 52$  over 116 in the three species) could be unambiguously classified by the ear as agonistic (27.6%) or affiliative (17.2%).

The context of these commenting calls was in most cases (92.3%) congruent with the agonistic or affiliative content of the social interaction attended by the calling bystander.

## Discussion

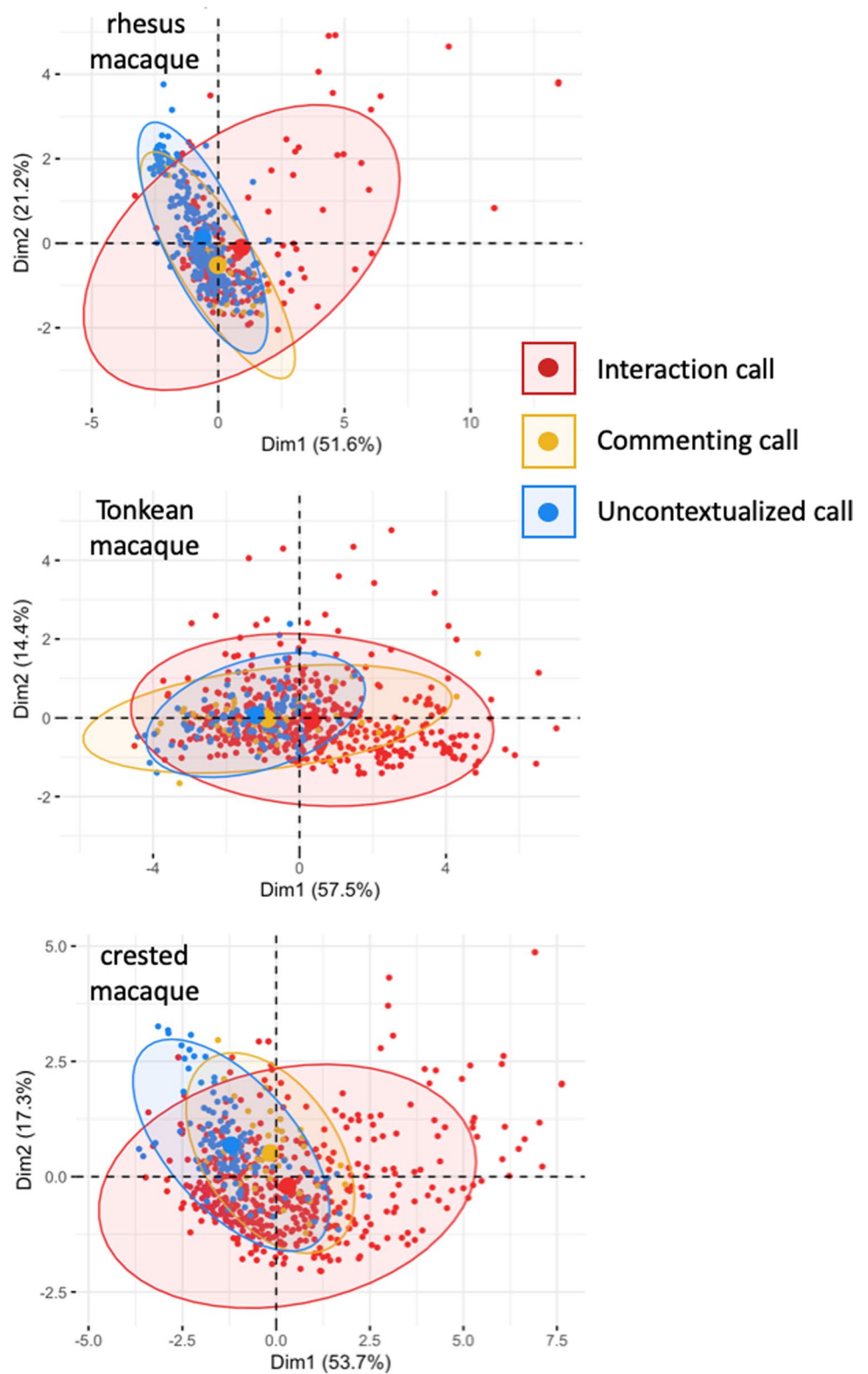
The comparison of several species of macaque revealed significant interspecific differences in the context specificity of their calls. We found that tolerant macaques had a higher degree of freedom than intolerant macaques in the association between vocal structure and social context. It also appears that the form of commenting calls was more differentiated in Tonkean and crested macaques than in rhesus macaques. These results on contextual flexibility in vocal signal production were made possible by using quantitative methods based on Shannon's information theory. They significantly extend the conclusions of a previous study on structural diversity and flexibility in vocal signal production (Rebout et al. 2020).

Analysis of the context specificity of calls showed greater relative uncertainty values in Tonkean and crested macaques than in Japanese and rhesus macaques. This finding implies either that the calls emitted in different contexts had closer acoustic structures in tolerant than in intolerant macaques or that calls typically associated with a given context—agonistic, affiliative or neutral—were less strongly associated with that context in the former species than in the latter species. In both cases, this means that there was more uncertainty in vocal signalling in tolerant macaques than in their intolerant counterparts. The strength of the regularities between the signal and its context of emission influences the extent to which the listener can obtain accurate information from the signal; the less context-specific a signal is, the more additional information is needed by the listener about the context to give it meaning (Smith 1977; Seyfarth and Cheney 2003; Wheeler and Fischer 2012). From the degree of freedom between vocal structure and occurrence context, we can deduce the potential range of meanings in the communicative repertoire of a species. The looser association found between structure and context in tolerant macaques indicates that their vocal communication system may involve a greater variety of meanings compared to intolerant macaques.

In intolerant species such as Japanese and rhesus macaques, it can be said that individuals experience clear-cut social situations. As previously mentioned, dominance and kinship rule their social life, interindividual conflicts most often end in clear winners and losers, and subordinates commonly direct formal signs of submission at higher-ranking individuals (Preuschoft and Schaik 2000; Thierry 2000, 2007; Rebout et al. 2017). This is consistent with the use of context-specific signals, capable of providing listeners with precise information with only a minimum of contextual



**Fig. 2** Acoustic distances between interaction, commenting and uncontextualized calls for three species of macaque: first factorial plane with the three centroids of call categories on the first two principal components (Dim1 & Dim2). The ellipses correspond to the 95% confidence interval



cues, as documented by Gouzoules and collaborators (Gouzoules et al. 1984, 1998) for rhesus macaque scream vocalizations (see also Mercier et al. 2019 for vervets, *Chlorocebus pygerythrus*). In comparison, the outcome of the social

interactions of tolerant species such as Tonkean and crested macaques cannot be easily predicted from their dominance and kinship relationships, they have better skills than intolerant macaques in the social domain, and they often switch

quickly from aggression to flight, protest, or reconciliation (Thierry et al. 1994; Thierry 2000, 2007; Dubosq et al. 2014; Joly et al. 2017). In such circumstances, the use of signals that are weakly dependent on context leaves a great deal of uncertainty in the information content. Flexible calls add richness to communication, offering a wide range of expression that can allow receivers to better manage ambiguous social situations. It should be noted, however, that rhesus macaques differed significantly from Japanese macaques. It could be proposed that this difference is explained by different levels of social tolerance in these two species, but this hypothesis appears unlikely given the proximity of both species in terms of social relationships (Thierry 2007). We cannot exclude that the contrast found between both species is due to the intervention of another unknown factor, such as the proportion of kin-related individuals in each group for example.

The study of commenting calls lends an additional dimension to these results by examining the ability of individuals to distance themselves from their immediate context and communicate as third parties about the interactions of their group mates (Brumm et al. 2005; see Schamberg et al. 2018). In rhesus macaques, the vocal performances of interacting individuals were distinct from those not directly involved in social interactions. In contrast, no differences were observed in the structure of their uncontextualized and commenting calls, indicating that the latter do not convey additional information. In more tolerant species such as Tonkean and crested macaques, interaction calls diverged from commenting calls—albeit non-significantly in crested macaques—and we found marked discrepancies between uncontextualized and commenting calls. The latter therefore appear to be well differentiated comments from bystanders on outgoing events. Their meaning was generally in agreement with the context of the observed interaction. Not only can the callers alert other group members, but by expressing their emotional response and/or likely future behaviour remotely while witnessing a social interaction (Waller et al. 2016, 2017), they can also transmit filtered information about its content. There are indications that Tonkean and crested macaques have a particularly strong commitment to the behaviour of others, associated with frequent polyadic interactions (Petit and Thierry 1994, 2000; Petit et al. 2008; Palagi et al. 2014; Puga-Gonzalez et al. 2014). The information conveyed by commenting calls may contribute to this pattern and enhance social cohesion by adding communicative feedback at the collective level.

It may be noted that there is only limited interest in providing specific comments on interactions whose outcome is foreseeable, as is the case with rhesus macaques. On the contrary, when results remain uncertain—as observed in more tolerant species—the diffusion of information within the group through circumstantial comments can be beneficial

in the same way that food calls disseminate information on food availability (Hauser and Marler 1993; Clay and Zuberbühler 2009). Moreover, our results point to a possible link between communicative flexibility and emotional expressiveness, in accordance with Morton's 'motivation-structural hypothesis' (1977), which states that a wide range of sounds corresponds to more numerous points along motivation gradients and quick changes in motivation. A low degree of association between structure and function in tolerant macaques can allow signallers to gradually move from one call to another and express a broad spectrum of emotions and intentions in a given context (Freeberg et al. 2012).

Using uncertainty as an indicator of complexity, our results support both predictions of the social complexity hypothesis for communicative complexity regarding the context specificity of calls and the form of commenting calls. Species with a higher degree of uncertainty in social interactions (i.e. social complexity) were also those with a lower degree of association between acoustic structure and social context and therefore uncertainty in vocal signals (i.e. vocal complexity). This is consistent with the findings of a previous study where we examined the relationship between the diversity of macaque vocal signals (number of call categories) and the flexibility of their acoustic structure (degree of gradation between call categories), showing that the diversity and flexibility of the acoustic structure of vocal signals were greater in species that display a higher degree of social complexity (Rebout et al. 2020). In the present study, we addressed another dimension of vocal complexity, that of contextual flexibility. The relationship found between the acoustic structure of the calls and their context of emission points to a link between the contextual flexibility of vocal signals and the level of uncertainty in the social style of macaques. Taken together, these results reveal that the vocal signals of more tolerant and socially complex macaques have a greater information potential than those of less tolerant and socially complex macaques, likely due to a higher degree of gradation of signals and a higher degree of freedom in the association between acoustic structure and social context. It should be noted that causal direction is still under discussion regarding the social complexity hypothesis (Peckre et al. 2019). Complex social situations may require complex communicative abilities. However, complex communicative abilities may also contribute to the emergence of complex social situations. These two processes are unlikely to be mutually exclusive.

The physical structure of habitats may affect variables such as the amplitude and frequency of auditory signals (Waser and Brown 1986; Hauser 1996), but we do not know of any variations in the ecological environment of macaques that could explain the interspecific differences we have highlighted. It may be added that we have investigated the vocalizations of three species in captive conditions, and in the wild for a fourth species, but we have

not found any contrasts between the species that could be attributed to the conditions of recording. Phylogenetic relatedness between species is another possible confounding factor. Japanese and rhesus macaques on the one hand and Tonkean and crested macaques on the other belong to two different macaque lineages, respectively (Fooden 1980; Tosi et al. 2003). One may wonder to what extent this could account for the contrasts observed between the two pairs of species. However, the measurement of acoustic distances between call categories gave rise to cross-species contrasts that could not be explained by phylogenetic relationships between species (Rebout et al. 2020). Future research should expand the analyses to more groups and species to confirm our current conclusions. In particular, the data needed to analyse the commenting calls were only available for one intolerant macaque species; other intolerant species have to be studied to further test the association between the acoustic structure of commenting calls and levels of social tolerance. The present study focused on the communication potential of the acoustic structure of macaque vocalizations in three main contexts. It would be interesting to extend the investigation to more specific categories of social contexts (see Gouzoules et al. 1984; Cheney and Seyfarth 2018). It is also necessary to address vocal signals such as commenting calls through playback experiments and test the ability of listeners to attribute meanings to comments that have different levels of context specificity.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03177-7>.

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**Data availability** The dataset generated and analysed in the study is available as supplementary material (ESM2).

## Declarations

**Ethics approval** The study followed the ASAB/ABS guidelines for the treatment of animals in behavioural research as published in *Animal*

*Behaviour* (2005, 69:i–vi). It complied with the legal requirements of the French, Italian, Dutch, Japanese and Indonesian governments. Research was observational and did not include any experimental intervention, so no review by an ethics committee was required.

**Conflict of interest** The authors declare no competing interests.

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