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▶ **To cite this version:**

Nancy Rebout, Arianna de Marco, Jean-Christophe Lone, Andrea Sanna, Roberto Cozzolino, et al.. Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication. Proceedings of the Royal Society B: Biological Sciences, 2020, 287 (1928), pp.20200439. 10.1098/rspb.2020.0439 . hal-02863271

HAL Id: hal-02863271
https://hal.science/hal-02863271

Submitted on 10 Jun 2020

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Rebout, N., De Marco, A., Lone, J.-C., Sanna, A., Cozzolino, R., Micheletta, J., Sterck, E. H. M., Langermans, J. A. M., Lemasson, A., & Thierry, B. (2020). Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication. Proceedings of the Royal Society B: Biological Sciences, 287(1928), 20200439.

https://doi.org/10.1098/rspb.2020.0439

Author-supplied statements

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Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
Research was observational. It complied with the legal requirements and guidelines of the Italian, French Japanese, Dutch and Japanese governments, and followed the ASAB/ABS guidelines for the treatment of animals in behavioural research

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
The dataset is available at the Dryad Digital Repository
https://doi.org/10.5061/dryad.905qfttgw

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable):
CUST_STATE_CONFLICT :No data available.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
Experimental design: N.R., B.T., A.L.; animal management: A.D.M., A.S., J.A.M.L., E.H.M.S.; data collection: N.R., A.D.M., A.S., A.L., J.M.; data analysis: N.R, A.D.M, A.S, J.C.R.; manuscript writing: N.R., B.T.; critical comments and additions to the manuscript: all authors; funding: R.C.

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Tolerant and intolerant macaques show different levels of structural complexity in their vocal communication

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Running title: Vocal complexity in macaques

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Abstract

We tested the social complexity hypothesis which posits that animals living in complex social environments should use complex communication systems. We focused on two components of vocal complexity: diversity (number of categories of calls) and flexibility (degree of gradation between categories of calls). We compared the acoustic structure of vocal signals in groups of macaques belonging to four species with varying levels of uncertainty (i.e. complexity) in social tolerance (the higher the degree of tolerance, the higher the degree of uncertainty): two intolerant species, Japanese and rhesus macaques, and two tolerant species, Tonkean and crested macaques. We recorded the vocalizations emitted by adult females in affiliative, agonistic, and neutral contexts. We analysed several acoustic variables: call duration, entropy, time and frequency energy quantiles. The results showed that tolerant macaques displayed higher levels of vocal diversity and flexibility than intolerant macaques in situations with a greater number of options and consequences, i.e. in agonistic and affiliative contexts. We found no significant differences between tolerant and intolerant macaques in the neutral context where individuals are not directly involved in social interaction. This shows that species experiencing more uncertain social interactions displayed greater vocal diversity and flexibility, which supports the social complexity hypothesis.

Keywords: acoustics, social system, social style, cluster analysis, comparison, primates

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1. Introduction

When looking for the determinants of social evolution in animals, two main types of factors can be distinguished: external pressures coming from the environment and internal constraints arising from the structure of the phenotype. Understanding how adaptation to environmental factors shapes social behaviour has attracted a great deal of research, and is in fact a main objective of the field of behavioural ecology [1,2]. In comparison, the role of structural constraints in biology has long been a controversial issue [3,4], and much less effort has been devoted to studying how they channel social organizations [5]. Although the definition of structural constraints itself has been problematic for some time, they can be actually defined as processes that limit the response of phenotypic traits to the selective action of ecological factors [6,7]. These constraints arise from the existence of functional relationships that link phenotypic traits or from passive interconnections that have occurred over the course of evolutionary history, and keep them in an entrenched state [5,8,9].

According to the *social complexity hypothesis for communicative complexity*, there is a functional relationship between patterns of communication and patterns of social organisation: animals living in complex social environments should use complex communication systems because a complex social life increases the need to discriminate individuals, express a wide range of emotional states, and convey a broad variety of messages related to different goals and contexts [10–12]. Although the social complexity hypothesis applies to communicative signals in general, most of the current evidence comes from the study of vocal communication [10]. The correlations found between the amount of information or the size of vocal repertoire on one side, and the size of social groups [13–15] or the number of categories of individuals on the other side [11,16] are in line with this hypothesis. However, there are problems with the definition and measurement of both social and vocal complexity.

There is no consensus on measures of the complexity of social systems [10,17–19]. The number of individuals in a social unit, as well as their number of categories or interactions, have long been used as indicators of complexity [10,11,16,17,20,21]. More recently, authors have focused on the number of social relationships or associations between group members [18,22]. Numbering the components of social systems may provide a good proxy for assessing their diversity, but diversity is only part of complexity, it does not encompass all aspects of

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complexity [23], which limits the evaluation of the social complexity hypothesis.

A similar problem hinders the measurement of the complexity of vocal communication [24]. Authors generally assume that the greater the number of call types, the higher the level of vocal complexity [14,15,25]. In these studies, what is considered is the diversity of communication signals rather than the complexity of the entire vocal system. Moreover, there is no agreement on how to identify the types of calls, and therefore the size of a species' communicative repertoire [24]. The task is especially tricky when repertoires are graded, that is, when there is gradual transition from one acoustic structure into another [24], as reported in species such as primates [26,27]. Some have proposed abandoning the idea of counting the number of calls to quantify vocal complexity, and instead using the degree of gradation of repertoires [24,28], i.e. flexibility in the acoustic structure of vocal signals. Since diversity and flexibility represent two different components of complexity, however, it seems that the best solution is to take both into account when characterising vocal complexity [23].

Uncertain outcomes appear to be the most important characteristic of complex systems [29,30]. Shannon's information theory [31] provides a way to quantify diversity and flexibility in terms of uncertainty [23]. This theory refers to what can be treated as a quantity of information which is here synonymous with a lack of *a priori* knowledge about the outcome of events, and therefore their unpredictability. More types of calls or more graded calls offer a greater number of options and, ultimately, the greater the number of options, the greater the uncertainty. The social complexity hypothesis can therefore be tested by comparing the diversity and flexibility of communication in species with varying levels of uncertainty in their social relationships. These species must be close enough to allow for homologous comparison from the point of view of both social relations and communication signals. In this respect, the genus *Macaca* offers a model that meets these requirements. Macaque species exhibit wide variations in their degree of social tolerance, which can be related to different levels of uncertainty in the outcome of their agonistic interactions [32,33]. In the most intolerant species, social conflicts generally have clear consequences: in Japanese macaques (*Macaca fuscata*) and rhesus macaques (*M. mulatta*), for instance, the recipient of aggression flees or submits in nine out of ten cases among unrelated females [34]. By contrast, in more tolerant species the recipient of the aggression frequently protests or counter-attacks: in Tonkean

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macaques (*M. tonkeana*) and crested macaques (*M. nigra*), 68.0 and 45.4% of conflicts among unrelated females, respectively, remain undecided, with no clear winners and losers [34].

The need for complex communication signals is not necessarily the same in all social contexts [10]. In the agonistic context, animals need information to cope with the many potential outcomes of uncertain situations such as open contests between two or more individuals, which affects competition for resources and expose individuals to risk of injury. In the affiliative context, a wealth of communication signals can also help individuals to achieve the best solution from a variety of behavioural options and maintain their social relationships [25,35]. Significant interspecies differences in communication systems are to be expected in situations of competition and cooperation. On the contrary, no significant interspecies differences should occur in neutral circumstances – i.e. when individuals are not directly involved in a social interaction – that do not require the expression of a wide range of intentions.

The interspecific variations reported in the agonistic patterns of macaques covary with other components of their social style such as hierarchical steepness, degree of nepotism, reconciliation rates, or range of facial displays; for example, dominance and kinship relations have stronger influence on individual behaviours in intolerant macaques compared with tolerant macaques, and the latter reconcile more often and have a greater number of facial displays than the former [32,36,37]. Despite such variations, macaque species share the same basic patterns of organization. All are semi-terrestrial primates living in multimale-multifemale groups; males disperse, and females remain in their natal group where they constitute matrilines, i.e. subgroups of relatives linked by maternal descent [36]. While no association has been found so far between the contrasting social styles of macaque species and the ecological conditions in which they have evolved, it appears that social styles consistently vary with phylogeny: closely related species are more similar than those that are distant [5,37,38].

In this study, we compared the vocal signals of two tolerant species (Tonkean & crested macaques, *Macaca tonkeana & M. nigra*) and two intolerant species (Japanese & rhesus macaques, *M. fuscata & M. mulatta*), based on three main variables (acoustic distance, diversity, flexibility) in three different social contexts (agonistic, affiliative, neutral). Like the other species of macaque, they use a graded repertoire of vocalizations [39–42]. They are

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mainly frugivorous and their primary habitat is forest, with the exception of rhesus macaques which occur in a variety of habitats, from forests to arid lands or regions of human settlement [38]. Both Tonkean and crested macaques live on different parts of the island of Sulawesi, Indonesia, they belong to the oldest macaque lineage [43]. Japanese and rhesus macaques live in Japan and mainland southern Asia, respectively, and both belong to a more recent lineage [43,44]. The two lineages separated about five million years ago [45,46]. In comparison, the divergence between Tonkean and crested macaques on one side, and Japanese and rhesus macaques on the other side, is much more recent. It is estimated to have occurred almost one million years ago at the latest [46,47]. Because of these phylogenetic distances, it can be expected that the vocal signals used by individuals will differ more between these two pairs of species than within each pair. However, such differences should apply indiscriminately to the various vocal variables and social contexts, contrary to the social complexity hypothesis which specifies that contrasts between species should depend on the variables and contexts.

We tested the predictions of three different hypotheses: (1) *Null hypothesis*: We should find no significant difference in the calls of tolerant and intolerant species regardless of variables and contexts; (2) *Phylogenetic hypothesis*: Greater similarity should occur in more closely related species, for any variable, and regardless of the social context, so we should find more differences between Tonkean and crested macaques on the one hand, and Japanese and rhesus macaques on the other, than within each of these species pairs across variables and contexts; (3) *Social complexity hypothesis*: Greater uncertainty in the social interactions of tolerant species compared to intolerant species should be associated with greater vocal diversity and flexibility in the former species than in the latter, while no significant differences should be found regarding the acoustic distances of calls. In addition, differences in diversity and flexibility should vary across social contexts: they should be strong in the agonistic and affiliative contexts, and weak in the neutral context.

2. Methods

(a) Subjects and living conditions

We made behavioural observations and acoustic recordings in 29 adult females from two groups of Japanese macaques, 16 adult females from two groups of rhesus macaques, 13 adult

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169 females from four groups of Tonkean macaques, and 51 adult females from two groups of
170 crested macaques. We focused on adult females because they are the most represented age-and-
171 sex category in macaque social groups, and also the most active contributors in vocal
172 communication [48]. Japanese, rhesus and Tonkean macaque females were captive born and at
173 least five years old. Crested macaques were studied in their natural habitat, and the age of the
174 subjects was assessed according to their reproductive history since 2006 (Macaca Nigra
175 Project, www.macaca-nigra.org), their body size, the shape of their nipples, and the presence of
176 old physical injuries. The composition of groups is given in Supplementary material S1,
177 Table 1.

178 The groups of Japanese macaques (Ft, Fw) were housed in two enclosures of 960 and
179 4,600 m², respectively, at the Primate Research Institute in Inuyama, Japan [49]. The groups of
180 rhesus macaques (Ma, Mb) were housed in two 210-m² enclosures at the Biomedical Primate
181 Research Center in Rijswijk, The Netherlands [50]. One group of Tonkean macaques (Tb) was
182 housed at the Orangerie Zoo in Strasbourg, France, in a 120-m² enclosure, and the other three
183 groups (Tc, Td, Te) were housed at the Parco Faunistico di Piano dell'Abatino Rescue Centre
184 in Rieti, Italy, in 500-m² enclosures [50]. Enclosures were wooded or furnished with perches,
185 ropes and shelters. Animals were fed commercial monkeys diet pellets, supplemented with
186 fresh fruits and vegetables, and water was available ad libitum. The groups of crested
187 macaques (Npb, Nr1) lived in the Tangkoko Nature Reserve, North Sulawesi, Indonesia [35].
188 They were not provisioned and inhabit lowland tropical rainforest [51].

189 The study complied with the legal requirements and guidelines of the Italian, French
190 Japanese, Dutch and Japanese governments, and followed the ASAB/ABS guidelines for the
191 treatment of animals in behavioural research. In what follows we will refer for convenience to
192 the Tonkean and crested macaque species as the Tonkean/crested pair, and the Japanese and
193 rhesus macaque species as the Japanese/rhesus pair.

194

195 **(b) Data collection**

196 We carried out observations outdoor to ensure the quality of the recordings. Data were
197 collected by A.L. in Japanese macaques [49], N.R. in rhesus macaques, A.D.M., A.S. and N.R.
198 in Tonkean macaques [50], and J.M. in crested macaques [35] (S1, Table 1). We observed

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199 subjects in a predefined random order using focal sampling. Sample duration was 10 min in
200 Japanese and Tonkean macaques from groups Tc, Td and Te, 15 min in rhesus macaques and
201 Tonkean macaques from group Tb, and 30 min in crested macaques. This resulted in
202 6.1±0.16 h of focal sampling per female in Japanese macaques, 12.7±0.7 h in rhesus macaques,
203 13.6±3.2 h in Tonkean macaques, and 7.8±0.4 in crested macaques.
204 In Japanese macaques, we recorded vocalizations with a TCD-D100 Sony (Tokyo, Japan)
205 DAT recorder (WAV format, sampling frequency: 44100 Hz, resolution: 16 bits), and an
206 ECM672 Sony directional microphone. In rhesus and Tonkean macaques, we used a Marantz
207 (Eindhoven, The Netherlands) PMD661 recorder (WAV format, sampling frequency:
208 44100 Hz, resolution: 16 bits), and a Sennheiser (Wedermark, Germany) K6 & ME66
209 directional microphone. In crested macaques, we used partly a high-resolution camera
210 Panasonic (Osaka, Japan) HDC-SD700 linked to a Sennheiser (Wedermark, Germany) K6 &
211 ME66 directional microphone, and partly a Marantz (Eindhoven, The Netherlands) PMD661
212 (WAV format, sampling frequency: 32000 Hz, resolution: 16 bits). We collected observational
213 data about the context of call emission with a lavalier microphone connected to the recorder in
214 Japanese, rhesus and Tonkean macaques (at805f, audio-technica, Leeds, UK vs TCM160,
215 Meditec, Singapore). In the crested macaques, the observer filmed the focal individual while a
216 field assistant recorded contextual data using a handheld computer; we extracted the audio
217 tracks from the video recordings using the software *FFmpeg* (v 3.4.1).
218 We distinguished three social contexts: agonistic, affiliative and neutral. Contexts were
219 defined according to the behaviours that could occur in the 3 s before and after the emission of
220 a call or a sequence of calls. A sequence was itself defined as a series of calls separated by a
221 maximum of 3 s. Note that behaviour patterns could fluctuate before and after the emission of
222 the calls, but the context did not change. Behavioural units were based on published repertoires
223 for macaques [52–54]. The agonistic context included aggression (supplantation, lunge, chase,
224 slap, grab, bite, facial threat display) and response to aggression (aggression, avoidance, flight,
225 crouch, submissive facial displays). The affiliative context included affiliative behaviours
226 (approach, sitting in contact, social grooming, social play, grasp, embrace, mount, affiliative
227 facial display). In the neutral context, the caller was not involved in a social interaction.
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(c) Acoustic analysis

We had records for 1368 calls in Japanese macaques, 1026 calls in rhesus macaques, 1210 calls in Tonkean macaques, and 1234 calls in crested macaques. The first author (N.R.) drew spectrograms using the software Raven Pro v1.4' (Cornell Lab of Ornithology, Center for Conservation Acoustics, Ithaca, NY, USA) with a 256 fast Fourier transform length and a Hanning window. With the same software, she measured the following variables: *Duration*: duration from the beginning to the end of a call, in seconds; *Q2 ratio*: ratio between duration that divides a call into two intervals of equal energy and duration in percentage; *Q1 frequency*: value of the frequency that divides a call into two intervals containing 25% and 75% of the energy, in Herz; *Q2 frequency*: value of the frequency that divides a call into two intervals of equal energy, in Herz; *Q3 frequency*: value of the frequency that divides a call into two intervals containing 75% and 25% of the energy, in Herz; *Wiener's aggregate entropy*: degree of disorder (i.e. noisiness) of the call, which uses 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. Our objective was to compare the four species on tonal and atonal calls, so we did not take into account the variables associated with fundamental frequencies since they are absent in atonal calls.

We selected recordings according to their quality. We randomly selected no more than three calls per sequence. A sequence was defined as a series of calls separated by a maximum of 3 s. Based on the total number of calls, females with a sample size less than five calls were excluded from the analysis. We also excluded some specific types of calls for which we could collect only a few recordings or none in each species: alarm calls, œstrus calls, and twits and cackles. Our samples resulted in 434 calls in 24 Japanese macaques (agonistic context: total number of calls, 79 & mean number of calls per female ± *SD*, 3.30 ± 377; affiliative context: 94 & 3.92 ± 4.16; neutral context: 255 & 10.6 ± 5.48), 639 calls in 16 rhesus macaques (agonistic: 118 & 7.38 ± 6.75; affiliative: 59 & 3.69 ± 3.22; neutral: 461 & 28.8 ± 16.0), 700 calls in 13 Tonkean macaques (270 & 20.8 ± 26.3, 226 & 17.4±14.3, 202 & 15.5 ± 8.42), and 696 calls in 19 crested macaques (201 & 10.6 ± 6.61, 297 & 15.6 ± 11.8, 191 & 10.1 ± 7.40).

(d) Statistical analysis

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Statistical analyses were run in *R* [55]. In a first analysis, we tested the differences in acoustic variables between species. In a second analysis, we assessed vocal diversity and compared it across species; we first performed a Principal Component Analysis (PCA), then a cluster analysis using an algorithm adapted to the graded repertoire. In a third analysis, we quantified the degree of gradation of the repertoire based on assignment probabilities using a second cluster analysis.

Acoustic distances: To test the differences between species in their acoustic variables, we performed discriminant function analyses using the function *lda* of the package *MASS* [56]. Since a discriminant function analysis can be affected by the unit in which predictor variables are measured, we scaled the acoustic variables prior to analysis. As collinearity can bias the results of a linear discriminant analysis [57], we removed acoustic variables so that each Pearson pairwise correlation between acoustic variables was less than 0.7; a simulation study showed that this is the value above which collinearity begins to bias model estimates, and is consequently the most commonly used threshold [58]. We therefore included the following variables in the discriminant function analysis: duration, Q2 ratio, Q2 frequency, Average entropy. We used the function *PermuteLDA* from the package *multiDimBio* [59] to assess interspecific differences in acoustic variables that we name *acoustic distances*, which allowed to statistically determine whether the species were at different locations in the multivariate space [60]. The function *PermuteLDA* calculated the multivariate distances between the sets of calls of each species in each context, and determined whether they differed significantly using Monte Carlo randomization.

Principal Component Analysis: As individuals were described by multifactorial characteristics, we used Principal Component Analyses (PCA) to reduce the dimensionality of the data set and provide more stable clustering, which means that clustering outputs are less sensitive to outliers [61]. In addition, the PCA approach eliminates correlations between factors that can influence clustering. Prior to PCA, and per context for all species, we scaled the seven acoustic variables to obtain a standard deviation of one, and a mean of zero, using the *R* base function *scale* [55]. The PCAs per context were then performed using the *PCA* function of *FactoMineR* package [62]. We weighted each female according to her number of calls by applying the argument *row.w* of the PCA function to balance the contributions of the different

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females to the creation of the space. Eventually, we selected the number of dimensions that explained near 95% of the variance of the data.

Vocal diversity: It is possible to measure *vocal diversity* by the number of call types in the repertoire of a species [12]. We ourselves measured it using the number of main categories of calls (i.e. groups of calls with similar acoustic characteristics) as follows. There is more uncertainty in communication when individuals can emit more calls, i.e. when the number of groups of calls is large. We determined the diversity in groups of calls by quantifying the number of clusters that structured the data set. The greater the number of clusters, the greater the vocal diversity. To calculate the optimal number of clusters, we chose to apply Gaussian Mixture models (GMM) based on a clustering approach [63–65]. GMMs assume that the clusters come from a finite mixture of probability distributions, which allows each group to be described with a different volume, shape, and orientation. The distribution parameters must be computed, which has been done by an Expectation maximization (EM) algorithm. The best model was then selected based on the Bayesian Information Criterion (BIC) score. The BIC scoring of a GMM was performed using the function *Mclust* of the package *Mclust* [66]. We have considered only the optimal number of clusters defined by the best model. As we wanted to compare these optimums statistically between each of the species, we used a bootstrap procedure. We ran 100 bootstraps where 80% of the data was sampled per bootstrap.

Vocal flexibility: We can measure signal uncertainty as the degree of gradation between call types [23]. We named *vocal flexibility* the degree of gradation between calls: the higher vocal flexibility is, the greater is the potential for information transmission [12]. We used the probability for a single call to belong to the different clusters to measure the degree of gradation between clusters. Accordingly, we used the soft assignment from a fuzzy clustering algorithm over GMM because we aimed at avoiding shape, volume or orientations difference between groups that can affect the likelihood of membership to each cluster. We applied the function *fanny* from the package *cluster* [67]. We set the argument membership exponent at 1.2 because it was the highest value – giving a higher degree of fuzziness [68] – that did not lead to convergence issue. Each call was assigned a probability of belonging to each cluster (*N* probabilities per call for *N* clusters). Therefore, if a call had a probability of one to belong to cluster A, and of zero to belong to any other clusters, this call was considered as typical of

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cluster A. On the contrary, if a call had more evenly distributed probabilities, it was considered as an intermediate call between at least two different clusters. The higher the number of intermediates, the higher the degree of gradation between clusters. Hence, to quantify this degree, we could use the Shannon's entropy formula [31]: the higher the entropy, the more even the distribution across clusters. We calculated the entropy of each call. Entropy value was then transformed into a relative entropy value, i.e., the entropy divided by the logarithm of the number of clusters [69,70]. We then calculated the mean of these relative entropy values. This computation was performed for a number of clusters varying from 2 to 6 (optimal number of clusters range).

Statistical comparisons: We compared the optimal number of clusters between species with a generalised linear model using a Poisson family (GLM). We compared the entropy value (i.e. degree of gradation between clusters) using linear models (LM). We compared the full models (i.e. with species as predictor factor) to the null models (i.e. without species) by applying likelihood ratio tests (LRT) using the function *lrtest* of the package *lmtest* [71]. This allowed to assess whether the species factor had a significant effect. When species had a significant effect, we performed post-hoc tests to make pairwise comparisons using the function *emmeans* of the package *emmeans* [72].

3. Results

(a) Acoustic distance

In the agonistic context, pairwise comparisons in the multivariate acoustic distances yielded significant differences between species, except between Japanese and Tonkean macaques; the distances between rhesus and Tonkean macaques remained limited relative to other distances between species (Fig. 1 & S1, Table 2). In the affiliative context, comparisons also yielded significant differences, except between Japanese and rhesus macaques; the distances between Tonkean macaques and either Japanese or rhesus macaques were limited (Fig. 1 & S1, Table 2). In the neutral context, all pairwise comparisons produced significant differences, but distances between Japanese, rhesus and Tonkean macaques were limited; crested macaques were farther from the other species in the three contexts (Fig. 1 & S1, Table 2). As an outcome, no grouping appeared between the Tonkean and crested macaques on

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one side, and Japanese and rhesus macaques on the other side.

(b) Vocal diversity

In the agonistic context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 28.1$, $p < 0.001$), meaning that they differed in their number of groups of calls. Post-hoc tests revealed that the Tonkean/crested pair had a significantly greater number of clusters than the Japanese/rhesus pair; no significant differences were found between the two members of each pair (Tonkean/crested macaques pair; Japanese/rhesus pair) (Fig. 2 & S1, Table 3). In the affiliative context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 90.4$, $p < 0.001$). Post-hoc tests showed that the Japanese macaques had a significantly smaller number of clusters than the other species; rhesus macaques had a lower number of clusters than the Tonkean/crested pair although the difference was significant with the crested macaques and not with the Tonkean macaques; Tonkean and crested macaques did not differ in their numbers of clusters (Fig. 2 & S1, Table 3). In the neutral context, the mean optimal number of clusters differed significantly between species (LRT $\chi^2 = 88.3$, $p < 0.001$). Post-hoc tests revealed that rhesus macaques had a significantly greater number of clusters than the other species; Tonkean macaques had a similar number of clusters compared to crested macaques; Japanese macaques had a significantly smaller number of clusters than the other species (Fig. 2 & S1, Table 3).

We used the truncation of the mean optimal number (N) of clusters for each species and context to illustrate the optimal grouping of call types usually recognized in macaque species (see Supplementary materials S1, Table 4, and S2, 3D cluster graphs). Although call types such as screams, barks and coos were common to the four species, other types of calls were specific to species: girneys and growls in Japanese and rhesus macaques, and soft grunts, hard grunts and chuckles in Tonkean and crested macaques (S1, Table 4).

(c) Vocal flexibility

In the agonistic context, the mean entropy value was significantly different between species (LRT $\chi^2 = 1092$, $p < 0.001$), meaning that they varied in the degree of gradation between call types. Post-hoc tests showed that the strongest differences opposed the

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Japanese/rhesus pair to the Tonkean/crested pair, with the latter displaying higher entropies than the former. Additionally, Tonkean macaques had a higher entropy than crested macaques, and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2 & S1, Table 3). In the affiliative context, the entropy value was significantly different between species (LRT χ^2 = 679, $p < 0.001$). Post-hoc tests revealed that the strongest differences opposed the Japanese/rhesus pair to the Tonkean/crested pair, with the Tonkean/crested pair displaying a higher entropy than the Japanese/rhesus pair; crested macaques had a higher entropy than Tonkean macaques, and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2 & S1, Table 3). In the neutral context, the entropy value was significantly different between species (LRT χ^2 = 737, $p < 0.001$). Post-hoc tests revealed no clear pattern contrasting the Japanese/rhesus to the Tonkean/crested pairs; rhesus macaques had a higher entropy compared to the other species; Japanese macaques had a higher entropy compared to Tonkean and crested macaques, and crested macaques had a higher entropy than Tonkean macaques (Fig. 2 & S1, Table 3).

4. Discussion

Based on the comparison of the acoustic variables characterizing both tonal and atonal calls, we found that the vocalisations of the four species of macaques studied differed by several respects. Although call types such as screams, barks and coos were common to all of them, other types of calls were specific to species, consistently with the results of previous studies: girneys and growls in Japanese and rhesus macaques, and soft grunts, hard grunts and chuckles in Tonkean and crested macaques [39,40,73–75]. The analysis of the acoustic distances between the sets of calls recorded in each species for each context confirmed that each macaque species has its own acoustic repertoire [42]. In particular, we did not find any significant contrasts in acoustic distances that would allow to arrange the sets of calls of Japanese macaques and rhesus on one side, and Tonkean and crested macaques on the other side.

We addressed vocal diversity by identifying the optimal number of groups of calls in each species. This showed that the Japanese/rhesus pair differed from the Tonkean/crested pair in the agonistic context; the latter had one additional group of calls compared to the former. It

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should be emphasized that a group of calls does not represent a single type of calls, but generally includes several types. In other words, this means that the diversity of call types was more extensive in Tonkean and crested macaques compared to Japanese and rhesus macaques in the context of aggression. We found a similar pattern in the affiliative context, although the difference between rhesus and Tonkean macaques was not statistically significant. On the other hand, we did not find similar contrasts between the two pairs of species in the neutral context. We also examined vocal flexibility by analysing the degree of gradation between groups of calls. We found the same type of demarcation between the Japanese/rhesus and the Tonkean/crested pairs in the agonistic and the affiliative contexts. As for vocal diversity, no difference appeared in the neutral context between both pairs of species.

Based on the interspecies contrasts evidenced in the acoustic structure of calls, we can reject the null hypothesis that there should be no difference between the Tonkean/crested and Japanese/rhesus pairs. The phylogenetic hypothesis posits that closely related species should show generalised similarity in calls for any acoustic variable and social context. However, this fails to explain why the two pairs of species differed in the number of group of calls and the degree of gradation between calls, but not in their acoustic distances, nor why the contrasts were consistent in the agonistic and affiliative contexts, but not in the neutral context. By contrast, the social complexity hypothesis is able to account for these various results. This hypothesis predicts that only complexity variables – vocal diversity measured by the number of groups of calls and vocal flexibility measured by the degree of gradation – should differ between the Tonkean/crested and Japanese/rhesus pairs, and exclusively in the agonistic and affiliative contexts. Indeed, we found that species differences in the neutral context did not follow any pattern related to variations in the degree of social uncertainty between pairs of species. As callers do not receive specific responses from their group mates in the neutral context, the number of possible outcomes remain limited, and it is understandable that vocal complexity was not influenced by the species-specific style of social interactions.

The social interactions of tolerant macaque species are characterized by a higher degree of freedom than those of more intolerant macaques, as they are less constrained by kinship and dominance relations [76]. Functionally, a greater diversity of vocal signals and a marked gradation between them can provide richer and more nuanced meanings, as moving gradually

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439 from one display to another would allow the signals to express a broad motivational spectrum
440 [77]. In other words, such signals have the potential to contain a large amount of information
441 and convey a wide range of emotions and intentions. This would contribute to the developed
442 negotiation skills of tolerant macaques, enabling them to engage in highly sophisticated
443 affiliative interactions, manage undecided open contests, and achieve high rates of conflict
444 resolution [35,78–82].

445 It should be stressed that our results are by nature correlational. The causal direction of the
446 social complexity hypothesis for communicative complexity is still debated [12]. While
447 complex social situations may require complex communicative abilities, complex
448 communicative abilities may also foster the emergence of complex social interactions. Since
449 the two processes are not mutually exclusive, a positive feedback loop may occur between
450 them at the evolutionary level. In addition, it is generally assumed that the social complexity
451 hypothesis applies to entire social systems. Our results reveal that the hypothesis can hold for
452 some social situations and not for others. In particular, we did not find consistent differences
453 between tolerant and intolerant macaques in the neutral context, where most of the recorded
454 calls were coos and growls. As mentioned above, it is logical that no link between social and
455 communicative complexity has emerged in a context where callers were not involved in social
456 interactions.

457 We have studied the calls of three species of macaque in captive settings, and in the wild
458 for the fourth, but we found no contrast between groups that could be attributed to the
459 recording conditions. Furthermore, while Japanese, Tonkean and crested macaques are mainly
460 forest-dwelling species, rhesus macaques can live in quite diverse habitats. Again, our analyses
461 did not reveal systematic contrasts between rhesus macaques and the other three species. It is
462 known that the physical structure of the habitat can affect the frequency or amplitude of
463 auditory signals for example [26,83], but we have relied on variables related to vocal diversity
464 and flexibility, for which no influence of ecological conditions is assumed to date [10]. Future
465 research should confirm the contrasts in vocal diversity and flexibility found between tolerant
466 and intolerant macaques by extending the analyses to a larger number of groups and species.
467 The additional study of the combinations of calls in vocal sequences and the responses of
468 receivers will also be necessary to test the social complexity hypothesis in a comprehensive

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way.

Acknowledgements

We are grateful to the managers and keepers of the Parco Faunistico di Piano dell'Abatino (Rieti), the Orangerie Zoo (Strasbourg), the Biomedical Primate Research Center (Rijswijk) and the Primate Research Institute (Inuyama) for their valuable assistance. We thank S. Louazon and V. Biquand for their technical help, and F. Criscuolo and the Department Ecology, Physiology and Ethology (Strasbourg) for their financial contribution. Data collection in rhesus macaques was supported by an Eole Scholarships granted by the French-Dutch Network. Data collection in Japanese macaques was supported by the Japan Society for the Promotion of Science. Data collection in crested macaques was supported by the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA), the Department for the Conservation of Natural Resources (BKSDA, North Sulawesi), the staff of the Macaca Nigra Project, and the Agricultural University of Bogor.

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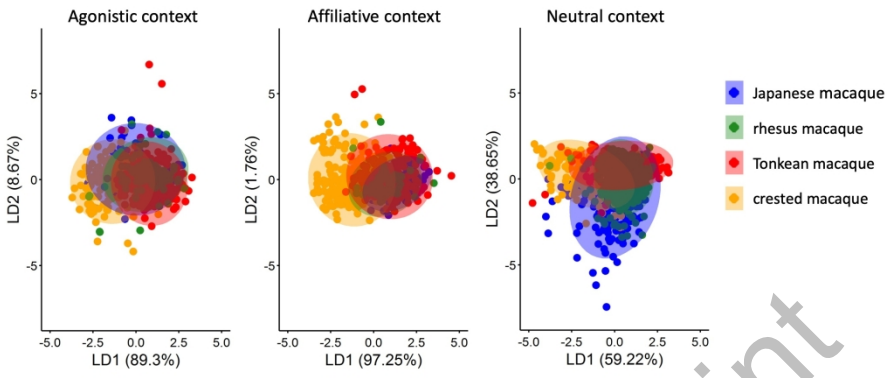
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Figures captions

Fig. 1. Comparisons of acoustic distances between species for calls emitted in the agonistic, affiliative and neutral contexts: Linear Discriminant Analysis biplot with the four groups centroids of species on the first two linear discriminants (LD1 & LD2). The ellipses correspond to the 95% confidence interval.

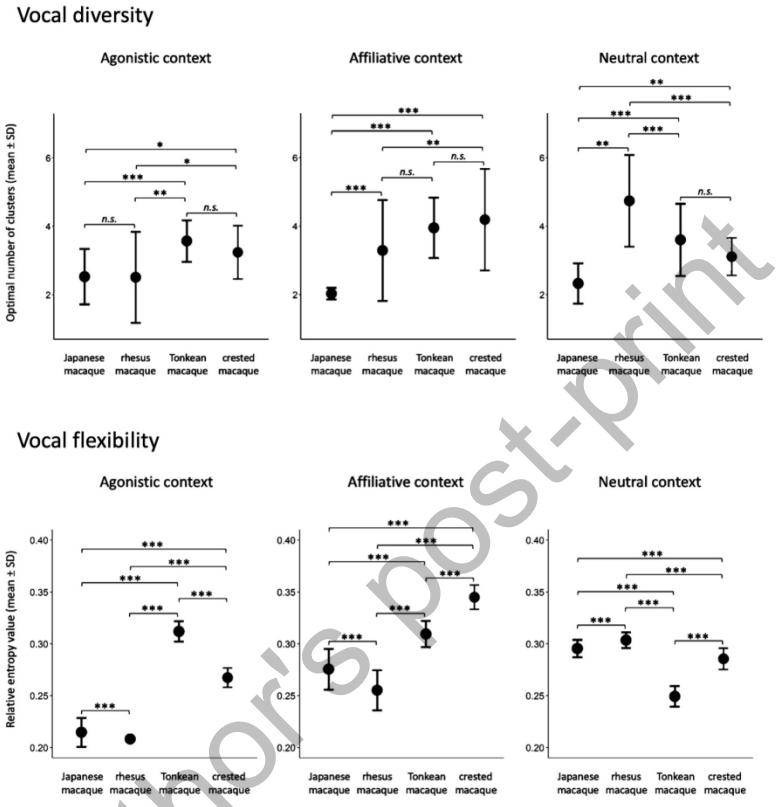
Fig. 2. Comparisons of vocal diversity and flexibility between species for calls emitted in the agonistic, affiliative and neutral contexts: optimal numbers of clusters and entropy values (***$p < 0.001$, ** $p < 0.01$, *$p < 0.05$).

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