1   **Tolerant and intolerant macaques show different levels of structural**

2   **complexity in their vocal communication**

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30 **Abstract**

31 We tested the social complexity hypothesis which posits that animals living in complex social

32 environments should use complex communication systems. We focused on two components of

33 vocal complexity: diversity (number of categories of calls) and flexibility (degree of gradation

34 between categories of calls). We compared the acoustic structure of vocal signals in groups of

35 macaques belonging to four species with varying levels of uncertainty (i.e. complexity) in

36 social tolerance (the higher the degree of tolerance, the higher the degree of uncertainty): two

37 intolerant species, Japanese and rhesus macaques, and two tolerant species, Tonkean and

38 crested macaques. We recorded the vocalizations emitted by adult females in affiliative,

39 agonistic, and neutral contexts. We analysed several acoustic variables: call duration, entropy,

40 time and frequency energy quantiles. The results showed that tolerant macaques displayed

41 higher levels of vocal diversity and flexibility than intolerant macaques in situations with a

42 greater number of options and consequences, i.e. in agonistic and affiliative contexts. We

43 found no significant differences between tolerant and intolerant macaques in the neutral

44 context where individuals are not directly involved in social interaction. This shows that

45 species experiencing more uncertain social interactions displayed greater vocal diversity and

46 flexibility, which supports the social complexity hypothesis.

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

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

80   A similar problem hinders the measurement of the complexity of vocal communication

81   [24]. Authors generally assume that the greater the number of call types, the higher the level of

82   vocal complexity [14,15,25]. In these studies, what is considered is the diversity of

83   communication signals rather than the complexity of the entire vocal system. Moreover, there

84   is no agreement on how to identify the types of calls, and therefore the size of a species'

85   communicative repertoire [24]. The task is especially tricky when repertoires are graded, that

86   is, when there is gradual transition from one acoustic structure into another [24], as reported in

87   species such as primates [26,27]. Some have proposed abandoning the idea of counting the

88   number of calls to quantify vocal complexity, and instead using the degree of gradation of

89   repertoires [24,28], i.e. flexibility in the acoustic structure of vocal signals. Since diversity and

90   flexibility represent two different components of complexity, however, it seems that the best

91   solution is to take both into account when characterising vocal complexity [23].

92   Uncertain outcomes appear to be the most important characteristic of complex systems

93   [29,30]. Shannon's information theory [31] provides a way to quantify diversity and flexibility

94   in terms of uncertainty [23]. This theory refers to what can be treated as a quantity of

95   information which is here synonymous with a lack of *a priori* knowledge about the outcome of

96   events, and therefore their unpredictability. More types of calls or more graded calls offer a

97   greater number of options and, ultimately, the greater the number of options, the greater the

98   uncertainty. The social complexity hypothesis can therefore be tested by comparing the

99   diversity and flexibility of communication in species with varying levels of uncertainty in their

100 social relationships. These species must be close enough to allow for homologous comparison

101 from the point of view of both social relations and communication signals. In this respect, the

102 genus *Macaca* offers a model that meets these requirements. Macaque species exhibit wide

103 variations in their degree of social tolerance, which can be related to different levels of

104 uncertainty in the outcome of their agonistic interactions [32,33]. In the most intolerant

105 species, social conflicts generally have clear consequences: in Japanese macaques (*Macaca*

106 *fuscata*) and rhesus macaques (*M. mulatta*), for instance, the recipient of aggression flees or

107 submits in nine out of ten cases among unrelated females [34]. By contrast, in more tolerant

108 species the recipient of the aggression frequently protests or counter-attacks: in Tonkean

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

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 and 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

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

subjects in a predefined random order using focal sampling. Sample duration was 10 min in Japanese and Tonkean macaques from groups Tc, Td and Te, 15 min in rhesus macaques and Tonkean macaques from group Tb, and 30 min in crested macaques. This resulted in 6.1±0.16 h of focal sampling per female in Japanese macaques, 12.7±0.7 h in rhesus macaques, 13.6±3.2 h in Tonkean macaques, and 7.8±0.4 in crested macaques.

In Japanese macaques, we recorded vocalizations with a TCD-D100 Sony (Tokyo, Japan) DAT recorder (WAV format, sampling frequency: 44100 Hz, resolution: 16 bits), and an ECM672 Sony directional microphone. In rhesus and Tonkean macaques, we used a Marantz (Eindhoven, The Netherlands) PMD661 recorder (WAV format, sampling frequency: 44100 Hz, resolution: 16 bits), and a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone. In crested macaques, we used partly a high-resolution camera Panasonic (Osaka, Japan) HDC-SD700 linked to a Sennheiser (Wedermark, Germany) K6 & ME66 directional microphone, and partly a Marantz (Eindhoven, The Netherlands) PMD661 (WAV format, sampling frequency: 32000 Hz, resolution: 16 bits). We collected observational data about the context of call emission with a lavalier microphone connected to the recorder in Japanese, rhesus and Tonkean macaques (at805f, audio-technica, Leeds, UK vs TCM160, Meditec, Singapore). In the crested macaques, the observer filmed the focal individual while a field assistant recorded contextual data using a handheld computer; we extracted the audio tracks from the video recordings using the software *FFmpeg* (v 3.4.1).

We distinguished three social contexts: agonistic, affiliative and neutral. Contexts were defined according to the behaviours that could occur in the 3 s before and after the emission of a call or a sequence of calls. A sequence was itself defined as a series of calls separated by a maximum of 3 s. Note that behaviour patterns could fluctuate before and after the emission of the calls, but the context did not change. Behavioural units were based on published repertoires for macaques [52–54]. The agonistic context included aggression (supplantation, lunge, chase, slap, grab, bite, facial threat display) and response to aggression (aggression, avoidance, flight, crouch, submissive facial displays). The affiliative context included affiliative behaviours (approach, sitting in contact, social grooming, social play, grasp, embrace, mount, affiliative facial display). In the neutral context, the caller was not involved in a social interaction.

(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

259   Statistical analyses were run in *R* [55]. In a first analysis, we tested the differences in

260   acoustic variables between species. In a second analysis, we assessed vocal diversity and

261   compared it across species; we first performed a Principal Component Analysis (PCA), then a

262   cluster analysis using an algorithm adapted to the graded repertoire. In a third analysis, we

263   quantified the degree of gradation of the repertoire based on assignment probabilities using a

264   second cluster analysis.

265   *Acoustic distances*: To test the differences between species in their acoustic variables, we

266   performed discriminant function analyses using the function *lda* of the package *MASS* [56].

267   Since a discriminant function analysis can be affected by the unit in which predictor variables

268   are measured, we scaled the acoustic variables prior to analysis. As collinearity can bias the

269   results of a linear discriminant analysis [57], we removed acoustic variables so that each

270   Pearson pairwise correlation between acoustic variables was less than 0.7; a simulation study

271   showed that this is the value above which collinearity begins to bias model estimates, and is

272   consequently the most commonly used threshold [58]. We therefore included the following

273   variables in the discriminant function analysis: duration, Q2 ratio, Q2 frequency, Average

274   entropy. We used the function *PermuteLDA* from the package *multiDimBio* [59] to assess

275   interspecific differences in acoustic variables that we name *acoustic distances*, which allowed

276   to statistically determine whether the species were at different locations in the multivariate

277   space [60]. The function *PermuteLDA* calculated the multivariate distances between the sets of

278   calls of each species in each context, and determined whether they differed significantly using

279   Monte Carlo randomization.

280   *Principal Component Analysis*: As individuals were described by multifactorial

281   characteristics, we used Principal Component Analyses (PCA) to reduce the dimensionality of

282   the data set and stabilize cluster results [61], which means that the clustering outputs are

283   smaller in number and less sensitive to noise and specific observations. In addition, the PCA

284   approach eliminates correlations between factors that can influence clustering. Prior to PCA,

285   and per context for all species, we scaled the seven acoustic variables to obtain a standard

286   deviation of one, and a mean of zero, using the *R* base function *scale* [55]. The PCAs per

287   context were then performed using the *PCA* function of *FactoMineR* package [62]. We

288   weighted each female according to her number of calls by applying the argument *row.w* of the

289 PCA function to balance the contributions of the different females to the creation of the space.

290 Eventually, we selected the number of dimensions that explained near 95% of the variance of

291 the data.

292   *Vocal diversity*: It is possible to measure *vocal diversity* by the number of call types in the

293 repertoire of a species [12]. We ourselves measured it using the number of main categories of

294 calls (i.e. groups of calls with similar acoustic characteristics) as follows. There is more

295 uncertainty in communication when individuals can emit more calls, i.e. when the number of

296 groups of calls is large. We determined the diversity in groups of calls by quantifying the

297 number of clusters that structured the data set. The greater the number of clusters, the greater

298 the vocal diversity. To calculate the optimal number of clusters, we chose to apply Gaussian

299 Mixture models (GMM) based on a clustering approach [63–665]. GMMs assume that the

300 clusters come from a finite mixture of probability distributions, which allows each group to be

301 described with a different volume, shape, and orientation. The distribution parameters must be

302 computed, which has been done by an Expectation maximization (EM) algorithm. The best

303 model was then selected based on the Bayesian Information Criterion (BIC) score. The BIC

304 scoring of a GMM was performed using the function *Mclust* of the package *Mclust* [66]. We

305 have considered only the optimal number of clusters defined by the best model. As we wanted

306 to compare these optimums statistically between each of the species, we used a bootstrap

307 procedure. We ran 100 bootstraps where 80% of the data was sampled per bootstrap.

308   *Vocal flexibility*: We can measure signal uncertainty as the degree of gradation between

309 call types [23]. We named *vocal flexibility* the degree of gradation between calls: the higher

310 vocal flexibility is, the greater is the potential for information transmission [12]. We used the

311 probability for a single call to belong to the different clusters to measure the degree of

312 gradation between clusters. Accordingly, we used the soft assignment from a fuzzy clustering

313 algorithm over GMM because we aimed at avoiding shape, volume or orientations difference

314 between groups that can affect the likelihood of membership to each cluster. We applied the

315 function *fanny* from the package *cluster* [67]. We set the argument membership exponent at 1.2

316 because it was the highest value – giving a higher degree of fuzziness [68] – that did not lead to

317 convergence issue. Each call was assigned a probability of belonging to each cluster (N

318 probabilities per call for N clusters). Therefore, if a call had a probability of one to belong to

319 cluster A, and of zero to belong to any other clusters, this call was considered as typical of

320 cluster A. On the contrary, if a call had more evenly distributed probabilities, it was considered

321 as an intermediate call between at least two different clusters. The higher the number of

322 intermediates, the higher the degree of gradation between clusters. Hence, to quantify this

323 degree, we could use the Shannon's entropy formula [31]: the higher the entropy, the more

324 even the distribution across clusters. We calculated the entropy of each call. Entropy value was

325 then transformed into a relative entropy value, i.e., the entropy divided by the logarithm of the

326 number of clusters [69,70]. We then calculated the mean of these relative entropy values. This

327 computation was performed for a number of clusters varying from 2 to 6 (optimal number of

328 clusters range).

329   *Statistical comparisons*: We compared the optimal number of clusters between species

330 with a generalised linear model using a Poisson family (GLM). We compared the entropy

331 value (i.e. degree of gradation between clusters) using linear models (LM). We compared the

332 full models (i.e. with species as predictor factor) to the null models (i.e. without species) by

333 applying likelihood ratio tests (LRT) using the function *lrtest* of the package *lmtest* [71]. This

334 allowed to assess whether the species factor had a significant effect. When species had a

335 significant effect, we performed post-hoc tests to make pairwise comparisons using the

336 function *emmeans* of the package *emmeans* [72].

337

338 **3. Results**

339 **(a) Acoustic distance**

340   In the agonistic context, pairwise comparisons in the multivariate acoustic distances

341 yielded significant differences between species, except between Japanese and Tonkean

342 macaques; the distances between rhesus and Tonkean macaques remained limited relative to

343 other distances between species (Fig. 1 & S1, Table 2). In the affiliative context, comparisons

344 also yielded significant differences, except between Japanese and rhesus macaques; the

345 distances between Tonkean macaques and either Japanese or rhesus macaques were limited

346 (Fig. 1 & S1, Table 2). In the neutral context, all pairwise comparisons produced significant

347 differences, but distances between Japanese, rhesus and Tonkean macaques were limited;

348 crested macaques were farther from the other species in the three contexts (Fig. 1 & S1,

349   Table 2). As an outcome, no grouping appeared between the Tonkean and crested macaques on

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

351

(b) Vocal diversity

353   In the agonistic context, the mean optimal number of clusters differed significantly

354   between species (LRT $\chi^2 = 28.1$, $p < 0.001$), meaning that they differed in their number of

355   groups of calls. Post-hoc tests revealed that the Tonkean/crested pair had a significantly greater

356   number of clusters than the Japanese/rhesus pair; no significant differences were found

357   between the two members of each pair (Tonkean/crested macaques pair; Japanese/rhesus pair)

358   (Fig. 2 & S1, Table 3). In the affiliative context, the mean optimal number of clusters differed

359   significantly between species (LRT $\chi^2 = 90.4$, $p < 0.001$). Post-hoc tests showed that the

360   Japanese macaques had a significantly smaller number of clusters than the other species; rhesus

361   macaques had a lower number of clusters than the Tonkean/crested pair although the difference

362   was significant with the crested macaques and not with the Tonkean macaques; Tonkean and

363   crested macaques did not differ in their numbers of clusters (Fig. 2 & S1, Table 3). In the

364   neutral context, the mean optimal number of clusters differed significantly between species

365   (LRT $\chi^2 = 88.3$, $p < 0.001$). Post-hoc tests revealed that rhesus macaques had a significantly

366   greater number of clusters than the other species); Tonkean macaques had a similar number of

367   clusters compared to crested macaques; Japanese macaques had a significantly smaller number

368   of clusters than the other species (Fig. 2 & S1, Table 3).

369   We used the truncation of the mean optimal number (N) of clusters for each species and

370   context to illustrate the optimal grouping of call types usually recognized in macaque species

371   (see Supplementary materials S1, Table 4, and S2, 3D cluster graphs). Although call types such

372   as screams, barks and coos were common to the four species, other types of calls were specific

373   to species: girneys and growls in Japanese and rhesus macaques, and soft grunts, hard grunts

374   and chuckles in Tonkean and crested macaques (S1, Table 4).

375

(c) Vocal flexibility

377   In the agonistic context, the mean entropy value was significantly different between

378   species (LRT $\chi^2 = 1092$, $p < 0.001$), meaning that they varied in the degree of gradation

13

between call types. Post-hoc tests showed that the strongest differences opposed the 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 2). In the affiliative context, the entropy value was significantly different between species (LRT $\chi^2 = 679$, $p < 0.001$). 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 2). In the neutral context, the entropy value was significantly different between species (LRT $\chi^2 = 737$, $p < 0.001$). 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 2).

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

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the agonistic context; the latter had one additional group of calls compared to the former. It 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 context, but not in the other social contexts. 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 in the agonistic and affiliative contexts. It also expects that the magnitude of contrasts between the two pairs of species should be absent in the neutral context. 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

15

439 dominance relations [76]. Functionally, a greater diversity of vocal signals and a marked

440 gradation between them can provide richer and more nuanced meanings, as moving gradually

441 from one display to another would allow the signals to express a broad motivational spectrum

442 [77]. In other words, such signals have the potential to contain a large amount of information

443 and convey a wide range of emotions and intentions. This would contribute to the developed

444 negotiation skills of tolerant macaques, enabling them to engage in highly sophisticated

445 affiliative interactions, manage undecided open contests, and achieve high rates of conflict

446 resolution [35,78–82].

447   It should be stressed that our results are by nature correlational. The causal direction of the

448 social complexity hypothesis for communicative complexity is still debated [12]. While

449 complex social situations may require complex communicative abilities, complex

450 communicative abilities may also foster the emergence of complex social interactions. Since

451 the two processes are not mutually exclusive, a positive feedback loop may occur between

452 them at the evolutionary level. In addition, it is generally assumed that the social complexity

453 hypothesis applies to entire social systems. Our results reveal that the hypothesis can hold for

454 some social situations and not for others. In particular, we did not find consistent differences

455 between tolerant and intolerant macaques in the neutral context, where most of the recorded

456 calls were coos and growls. As mentioned above, it seems logical that no link between social

457 and communicative complexity has emerged in a context where callers were not involved in

458 social interactions.

459   We have studied the calls of three species of macaque in captive settings, and in the wild

460 for the fourth, but we found no contrast between groups that could be attributed to the

461 recording conditions. Furthermore, while Japanese, Tonkean and crested macaques are mainly

462 forest-dwelling species, rhesus macaques can live in quite diverse habitats. Again, our analyses

463 did not reveal systematic contrasts between rhesus macaques and the other three species. It is

464 known that the physical structure of the habitat can affect the frequency or amplitude of

465 auditory signals for example [26,83], but we have relied on variables related to vocal diversity

466 and flexibility, for which no influence of ecological conditions is assumed to date [10]. Future

467 research should confirm the contrasts in vocal diversity and flexibility found between tolerant

468 and intolerant macaques by extending the analyses to a larger number of groups and species.

469 The additional study of the combinations of calls in vocal sequences and the responses of

470 receivers will also be necessary to test the social complexity hypothesis in a comprehensive

471 way.

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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 (***$p < 0.001$, ** $p < 0.01$, *$p < 0.05$).
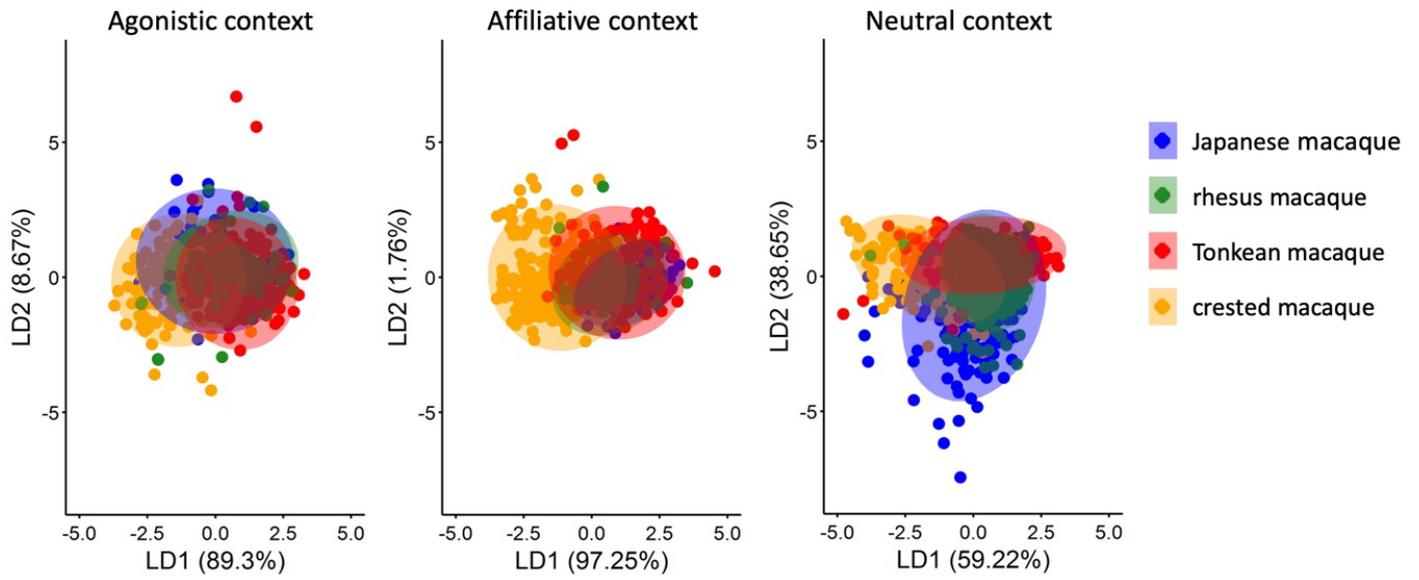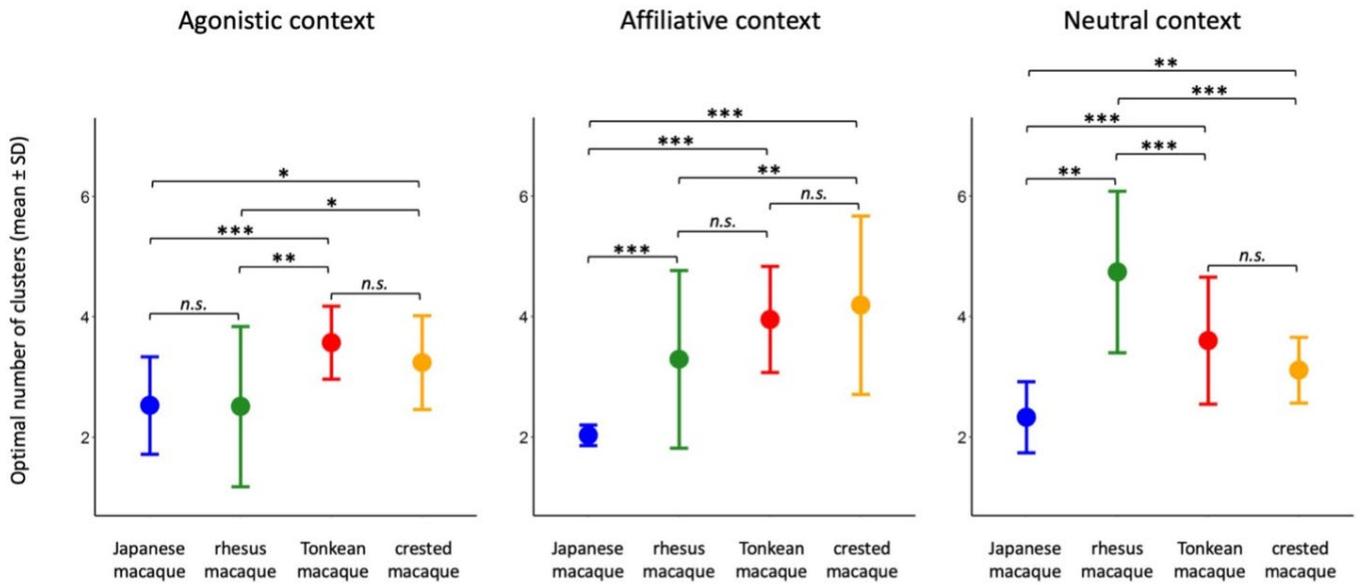
Fig. 1

Fig. 2

Vocal diversity

Vocal flexibility