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Ethics

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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

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

3

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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.

47
48 **Keywords:** acoustics, social system, social style, cluster analysis, comparison, primates

49 **1. Introduction**

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

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

73 There is no consensus on measures of the complexity of social systems [10,17–19]. The
74 number of individuals in a social unit, as well as their number of categories or interactions,
75 have long been used as indicators of complexity [10,11,16,17,20,21]. More recently, authors
76 have focused on the number of social relationships or associations between group members
77 [18,22]. Numbering the components of social systems may provide a good proxy for assessing
78 their diversity, but diversity is only part of complexity, it does not encompass all aspects of

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

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

111 The need for complex communication signals is not necessarily the same in all social
112 contexts [10]. In the agonistic context, animals need information to cope with the many
113 potential outcomes of uncertain situations such as open contests between two or more
114 individuals, which affects competition for resources and expose individuals to risk of injury. In
115 the affiliative context, a wealth of communication signals can also help individuals to achieve
116 the best solution from a variety of behavioural options and maintain their social relationships
117 [25,35]. Significant interspecies differences in communication systems are to be expected in
118 situations of competition and cooperation. On the contrary, no significant interspecies
119 differences should occur in neutral circumstances – i.e. when individuals are not directly
120 involved in a social interaction – that do not require the expression of a wide range of
121 intentions.

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

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

139 mainly frugivorous and their primary habitat is forest, with the exception of rhesus macaques
140 which occur in a variety of habitats, from forests to arid lands or regions of human settlement
141 [38]. Both Tonkean and crested macaques live on different parts of the island of Sulawesi,
142 Indonesia, they belong to the oldest macaque lineage [43]. Japanese and rhesus macaques live
143 in Japan and mainland southern Asia, respectively, and both belong to a more recent lineage
144 [43,44]. The two lineages separated about five million years ago [45,46]. In comparison, the
145 divergence between Tonkean and crested macaques on one side, and Japanese and rhesus
146 macaques on the other side, is much more recent. It is estimated to have occurred almost one
147 million years ago at the latest [46,47]. Because of these phylogenetic distances, it can be
148 expected that the vocal signals used by individuals will differ more between these two pairs of
149 species than within each pair. However, such differences should apply indiscriminately to the
150 various vocal variables and social contexts, contrary to the social complexity hypothesis which
151 specifies that contrasts between species should depend on the variables and contexts.

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

164

165 **2. Methods**

166 **(a) Subjects and living conditions**

167 We made behavioural observations and acoustic recordings in 29 adult females from two
168 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

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.

228

229 **(c) Acoustic analysis**

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

246 We selected recordings according to their quality. We randomly selected no more than
247 three calls per sequence. A sequence was defined as a series of calls separated by a maximum
248 of 3 s. Based on the total number of calls, females with a sample size less than five calls were
249 excluded from the analysis. We also excluded some specific types of calls for which we could
250 collect only a few recordings or none in each species: alarm calls, œstrus calls, and twits and
251 cackles. Our samples resulted in 434 calls in 24 Japanese macaques (agonistic context: total
252 number of calls, 79 & mean number of calls per female \pm SD, 3.30 ± 3.77 ; affiliative context:
253 94 & 3.92 ± 4.16 ; neutral context: 255 & 10.6 ± 5.48), 639 calls in 16 rhesus macaques
254 (agonistic: 118 & 7.38 ± 6.75 ; affiliative: 59 & 3.69 ± 3.22 ; neutral: 461 & 28.8 ± 16.0), 700
255 calls in 13 Tonkean macaques (270 & 20.8 ± 26.3 , 226 & 17.4 ± 14.3 , 202 & 15.5 ± 8.42), and
256 696 calls in 19 crested macaques (201 & 10.6 ± 6.61 , 297 & 15.6 ± 11.8 , 191 & 10.1 ± 7.40).

257

258 **(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 provide more stable clustering, which means that clustering outputs are less
283 sensitive to outliers [61]. In addition, the PCA approach eliminates correlations between
284 factors that can influence clustering. Prior to PCA, and per context for all species, we scaled
285 the seven acoustic variables to obtain a standard deviation of one, and a mean of zero, using the
286 *R* base function *scale* [55]. The PCAs per context were then performed using the *PCA* function
287 of *FactoMineR* package [62]. We weighted each female according to her number of calls by
288 applying the argument *row.w* of the *PCA* function to balance the contributions of the different

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

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

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

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

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

336

337 **3. Results**

338 **(a) Acoustic distance**

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

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

350

351 **(b) Vocal diversity**

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

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

374

375 **(c) Vocal flexibility**

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

379 Japanese/rhesus pair to the Tonkean/crested pair, with the latter displaying higher entropies
380 than the former. Additionally, Tonkean macaques had a higher entropy than crested macaques,
381 and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2 & S1, Table 3). In
382 the affiliative context, the entropy value was significantly different between species (LRT $\chi^2 =$
383 $679, p < 0.001$). Post-hoc tests revealed that the strongest differences opposed the
384 Japanese/rhesus pair to the Tonkean/crested pair, with the Tonkean/crested pair displaying a
385 higher entropy than the Japanese/rhesus pair; crested macaques had a higher entropy than
386 Tonkean macaques, and Japanese macaques had a higher entropy than rhesus macaques (Fig. 2
387 & S1, Table 3). In the neutral context, the entropy value was significantly different between
388 species (LRT $\chi^2 = 737, p < 0.001$). Post-hoc tests revealed no clear pattern contrasting the
389 Japanese/rhesus to the Tonkean/crested pairs; rhesus macaques had a higher entropy compared
390 to the other species; Japanese macaques had a higher entropy compared to Tonkean and crested
391 macaques, and crested macaques had a higher entropy than Tonkean macaques (Fig. 2 & S1,
392 Table 3).

393

394 **4. Discussion**

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

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

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

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

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

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

469 way.

470

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484

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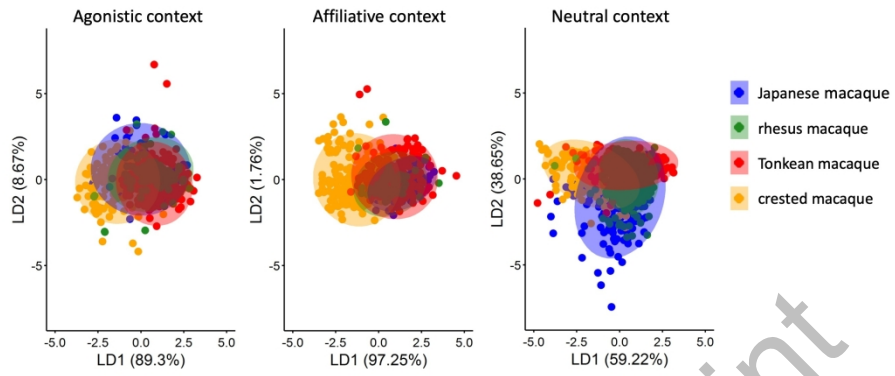
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Figures captions

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

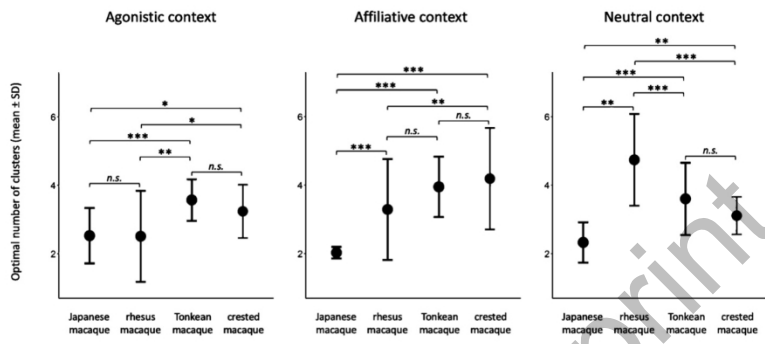
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Vocal diversity



Vocal flexibility

