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1 **Loud calls in male crested macaques (*Macaca nigra*)**

2 **– a signal of dominance in a tolerant species**

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5
6 **Running headline:** NEUMANN ET AL.: LOUD CALLS IN CRESTED MACAQUES

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26

27 Abstract:

28 Compared to other mammals, sexual signals occur particularly often within the primate order.
29 Nevertheless, little is known so far about the pressures under which these signals evolved. We
30 studied loud calls in wild crested macaques (*Macaca nigra*) in order to examine **whether**
31 **these are used as a sexual signal, particularly as a signal of dominance in this species.**
32 **Since the structure of loud calls may be influenced by the context in which they are**
33 **uttered, we tested for contextual differences in call structure.** Only males uttered loud
34 calls and analysis of 194 loud calls given from 15 males showed that call structure encoded
35 the caller's identity as well as his social status. Dominance rank was also reflected in the
36 frequency with which males called with alpha males calling most often. **The structure of**
37 **loud calls was however not influenced by context. Our findings consolidate the**
38 **assumption that in crested macaques, loud calls serve as a signal of dominance most**
39 **likely used to prevent contest between males for mates.** We herewith provide the first
40 direct evidence for a signal of dominance in a tolerant primate species and discuss more in
41 detail why this signal occurs only in one sex.

42

43 Key words: crested macaque, dominance signal, loud calls, *Macaca nigra*, sexual selection,
44 sexual signal, **social style**

45

46 The diversity of sexual signals occurring within the primate order intrigued Darwin (1876)
47 and is unique among mammals (e.g. Nunn 1999; Bradley & Mundy 2008). An acoustic signal
48 used in a variety of primate species that seems to function as a sexual signal at least in some
49 primate species is the loud call (synonymously called ‘long or long distance call’; Wich &
50 Nunn 2002). These vocalisations consist of loud, repetitive units and are usually uttered by
51 males (Gautier & Gautier 1977; Waser 1982; Mitani & Stuht 1998; Wich & Nunn 2002).
52 Although common in primates, the function of loud calls remains poorly understood.

53

54 From studies on other animal taxa, such as anurans, birds and ungulates, it is well
55 known that male acoustic signals play a role in male-male competition for mates (intra-sexual
56 selection) by signalling competitive abilities to contesters (e.g. Blanchard's cricket frog, *Acris*
57 *crepitans blanchardi*: Wagner 1992; red deer, *Cervus elaphus*: Reby et al. 2005) as well as in
58 attracting females (inter-sexual selection) by signalling individual quality to them (e.g. red
59 deer, *Cervus elaphus*: McComb 1991; gray tree frog, *Hyla versicolor*: Gerhardt et al. 2000;
60 red grouse, *Lagopus lagopus scoticus*: Mougeot et al. 2004).

61

62 For primates, in contrast, it has for a long time been assumed that loud calls have not
63 evolved through pressures of sexual selection, but are primarily used to mediate inter-group
64 spacing and intra-group cohesion (e.g. Riley 2005; da Cunha & Byrne 2006). Results of a
65 recent meta-analysis over the entire primate order however reveal that loud calls originally
66 served to defend resources and to attract mates (Wich & Nunn 2002), and thus presumably
67 still function in intra- and/or intersexual communication in a reproductive context. Although
68 direct evidence for this hypothesis is still missing, the few existing studies on the function of
69 loud calls lead to the conclusion that at least in some species, they represent a sexually
70 selected trait. In male chacma baboons (*Papio cynocephalus ursinus*) for example, loud calls
71 (‘wahoos’) signal dominance (Kitchen et al. 2003; Fischer et al. 2004) and play a role in male

72 agonistic interactions, e.g. during male-male chases, suggesting that wahoos serve a function
73 in male-male competition. In white-handed gibbons (*Hylobates lar*) and Thomas langurs
74 (*Presbytis thomasi*), loud calls signal a males pairing status (Raemaekers et al. 1984;
75 Reichard & Neumann 2007) and the life-phase he is in (see Steenbeek et al. 1999; Wich et al.
76 2003 for definition), respectively, suggesting that here, loud calls serve to attract females (but
77 see Mitani 1988) and in orangutans, male loud calls may serve both, male-male competition
78 and mate attraction (Delgado 2006). Apart from these studies, little is known about the
79 information content and potential function of these vocalisations and more studies are clearly
80 needed in order to better understand the adaptive significance of this trait in primates.

81
82 Crested macaques (*Macaca nigra*) are particularly interesting in this respect, since
83 they represent one of the few macaque species in which males utter loud calls (Wich & Nunn
84 2002). All macaque species share the same social system, living in multi-male multi-female,
85 female philopatric groups, but within the macaque genus, only species of the so called
86 silenus-lineage (with the exception of *Macaca nemestrina*, and *Macaca leonina*) exhibit loud
87 calls (Delson 1980; Tosi et al. 2003) raising the question why loud calls exist in these, but not
88 in other macaques. In addition, crested macaques seem to be the only calling macaque species
89 in which all adult males regularly vocalise whereas in the other macaques, calling is mainly
90 limited to alpha males (Baker et al. 1991; Okamoto 2001; Riley 2005). So far, macaque loud
91 calls have been interpreted to serve a function for inter-group spacing (Okamoto 2001),
92 within-group coordination (Riley 2005), species recognition (Muroyama & Thierry 1998)
93 and/or third party aggression intervention (Kinnaird & O'Brien 1999), but no study ever
94 examined the possibility that loud calls in Sulawesi macaques **are subject to** the pressures of
95 sexual selection.

96

97 Loud calls of crested macaques are also very interesting in a different context.
98 According to Thierry (2000, 2007), macaque species vary along a gradient of social styles,
99 mapped on a four-grade scale ranging from despotic to tolerant systems with crested
100 macaques belonging to the tolerant species (grade 4). Theoretical considerations led to the
101 predictions that despotic primate species should evolve signals of submission (i.e. low-
102 ranking individuals showing their subordination to higher-ranking ones) whereas tolerant
103 species should evolve signals of dominance (i.e. higher ranking individuals showing their
104 status to lower ranking individuals) or no status indicator, depending on the level of
105 asymmetry in dyadic conflicts and overall aggression intensity (Preuschoft & van Schaik
106 2000; Thierry 2004). Although there is ample evidence for signals of submission in despotic
107 (grades 1-2) and for signals of dominance in slightly tolerant macaques (grade 3; de Waal &
108 Luttrell 1985; Chaffin et al. 1995; Preuschoft 1995), there is to date no evidence for the
109 occurrence of dominance signals in any of the tolerant macaque (grade 4) species. Since
110 crested macaques belong to the group of tolerant macaques (Thierry 2000), it is particularly
111 interesting to investigate whether loud calls represent such a signal of dominance.

112

113 The aim of our study therefore was to investigate the information content of loud calls
114 in crested macaques in the light of two concepts: sexual selection theory and macaque social
115 style theory. Since crested macaques utter loud calls in different contexts (Kinnaird & O'Brien
116 1999) and the acoustic structure of these calls (and thus their information content and
117 function) may vary with context (like in chacma baboons; Fischer et al. 2002), we first
118 examined whether call structure varies in a context dependent manner. In a second step, we
119 investigated whether loud calls meet two major criteria for sexually selected signals, i.e.
120 whether the signal's expression is sexually dimorphic and whether there is variation in the
121 signal that can be assigned to individuals (Snowdon 2004). Furthermore, in order to
122 investigate whether loud calls signal male dominance, we examined the relationship between

123 the frequency of loud call utterance to selected acoustic call parameters and male dominance
124 rank. As a potential measure of male fighting ability and quality, the relationship between
125 male body weight, dominance rank and loud call characteristics were also examined. The
126 study was carried out on two wild groups of crested macaques living in the Tangkoko-
127 Batuangus Nature Reserve, North Sulawesi, Indonesia over a period of 14 months.

128

129

130 **METHODS**

131 **Study Site and Animals**

132 Data were collected on two groups of free ranging, wild crested macaques from July
133 2006 until August 2007 in the Tangkoko-Batuangus Nature Reserve, North Sulawesi,
134 Indonesia (1°33' N, 125°10' E). The reserve comprises an area of 8,867 ha lowland rainforest,
135 and ranges from sea level to 1,350 m (Collins et al. 1991; Rosenbaum et al. 1998). Two multi-
136 male groups ('R1' and 'R2') comprised 65-75 individuals each, including 7-10 and 9-10 adult
137 males, respectively. The ranging area of the study groups included undisturbed primary forest
138 as well as large areas of secondary forest and regenerating gardens with a severely damaged
139 canopy cover. The observed groups have been studied intermittently for more than ten years
140 (O'Brien & Kinnaird 1997; Reed et al. 1997; Kinnaird & O'Brien 1999) and were completely
141 habituated to human observers.

142

143 **Behavioural Data Collection**

144 We collected behavioural data on 23 males from the two groups using focal animal
145 sampling (Martin & Bateson 1993), resulting in 2743.5 hours of focal observation time (mean
146 focal hours per male: 119.3, range: 10.8 – 170.9, Table 1). Each male was followed once a
147 week, alternating from the male's descent from the sleeping tree until noon and from noon to
148 the time the focal male entered the sleeping tree. We used instantaneous sampling (Martin &

149 Bateson 1993) with a time interval of one minute **for the focal animal's activity**, noting the
150 occurrence of loud calls, **social interactions (socio-positive and agonistic behaviour,**
151 **mating)** and displacement interactions between males as continuous events. Agonistic and
152 displacement interactions **between males** were furthermore recorded ad libitum.

153

154 **Dominance Rank**

155 For rank allocation, we divided the study period into six distinct time periods, since group
156 composition varied over the course of the study due to migration events and maturation of
157 subadult males. Periods ranged from 49 to 92 days. During each period and for each group
158 separately, we created matrices containing dyadic dominance interactions (agonistic
159 interactions with unambiguous winner and loser, and displacement interactions (Thierry et al.
160 2000) for all adult males present during the given period. Only conflicts were taken into
161 account that did not include counter aggression by the 'victim/loser', i.e. only unidirectional
162 interactions.

163

164 We then tested whether it was justified to rank males linearly by means of de Vries'
165 (1995) h' index. The linearity indices have an average value of 0.72 (range: 0.53 – 0.94) and
166 the average p-value indicating whether linearity is different from what is expected by chance
167 is $p = 0.028$ (maximum $p = 0.069$). Even though 3 out of 12 hierarchies did not reach
168 statistical significance, we ranked males according to the I&SI method (de Vries 1998), with
169 rank 1 being the highest rank. Three hierarchies were found to contain inconsistencies, i.e. the
170 dyadic relationship between two males was reversed in the ordering produced by the
171 algorithm. Although in the two cases for which we have data, the inconsistencies predicted
172 the order in the subsequent time period, we created three rank classes: high (ranks 1 – 3),
173 middle (ranks 4 – 6) and low (ranks 7 – 10).

174

175 **Body Weight**

176 We weighed adult males. For this, a digital scale (modified Combics scale, Sartorius,
177 Göttingen, Germany, weight step = 0.02 kg) was positioned at a fixed location and single
178 males were lured onto the scale with a small amount of corn when a group was passing the
179 scale's position. Reading of the scale took place via a remote display. Measures were only
180 taken into account if a male was weighed at least twice during one weighing session.

181

182 **Vocal Recording & Acoustic Analysis**

183 Loud calls were recorded ad-libitum and the context in which the call occurred was
184 noted. Recordings were done with a digital portable solid state recorder (PMD660, Marantz,
185 Itasca, Illinois) and a directional microphone (K6-ME66, Sennheiser, Wedemark, Germany)
186 equipped with a windshield (265E, Rycote, Gloucestershire, UK) at a sampling rate of 44.1
187 kHz. We recorded a total of 194 loud calls of sufficient quality for analysis from six contexts:

- 188 • aggression = calls given during or immediately after an aggressive interaction, $N = 40$
- 189 • resting = calls given outside any obvious context, i.e. during resting periods, $N = 57$
- 190 • feeding = calls given during feeding or foraging activity, $N = 8$
- 191 • moving = calls given during group movement, $N = 13$
- 192 • social positive = calls that occurred in or followed affiliative interactions, such as
193 grooming, male-male mounting, genital grasp, $N = 12$
- 194 • mating = calls emitted during or shortly after copulation, $N = 64$

195

196 All calls were first inspected visually using SASLab Pro 4.39 (Avisoft Bioacoustics,
197 Berlin, Germany) to make sure that background noises (e.g. bird song and other individuals
198 calling) were not present in the recordings. The spectrogram settings that were applied for the
199 extraction were: FFT length = 1024 points, window = Hamming, frame size = 100%, overlap
200 = 96.87%. The resulting frequency resolution was 43 Hz at a time increment of 0.73 ms. After

201 down sampling the recordings to 22.05 kHz, frequency resolution was 22 Hz at a time
202 increment of 1.45 ms. All parameters were taken from down-sampled recordings, except
203 frequency range for which the original sampling rate was kept. For one parameter (dominant
204 frequency band), we applied a band pass filter to limit the frequency range of the signal, in
205 order to measure the band between 0.7 and 1.5 kHz ($f_{\text{high}} = 0.3$ kHz, $f_{\text{low}} = 2$ kHz, see Figure
206 1). All spectrograms were saved as ASCII files for further processing. We then measured
207 seven acoustic parameters: three temporal and four frequency parameters, which were suited
208 to describe structural variations in loud calls (for detailed description see Fig. 1 and Table 2).

209

210 **Statistical Analysis**

211 **We determined the general frequency with which loud calls were uttered in the**
212 **different contexts by first calculating the percentages with which each male called in the**
213 **different contexts (i.e. 100% = all calls of a single male) and subsequently calculating the**
214 **mean percentage over all males for each context.**

215

216 We conducted a mixed linear model to evaluate structural differences in male loud
217 calls related to rank and context. We used rank class and context as fixed factors and caller
218 identity and study group as random factor, and calculated tests for all seven acoustic
219 parameters. As study group did not improve our models, we excluded this factor from the
220 final models.

221

222 To describe individual differences in the structure of loud calls we conducted a
223 discriminant function analysis including all acoustic parameters. To validate the original
224 classification results of this analysis, we performed a cross validation using the leave-one-out
225 method. This method classifies each case based on functions derived by all but the one case.

226

227 To investigate the relation between call structure and body weight, we used
228 Spearman's rank correlation. For this, we calculated mean parameter values of all calls of a
229 given male while belonging to one rank class and used these means to correlate them with
230 body weight.

231

232 For each male, the mean frequency of call utterance (loud calls/hour) was calculated
233 and the influence of dominance rank class on this parameter was tested with a Kruskal-Wallis
234 test. To control for potential rank effects, we used data from the rank class for which most
235 observation time was gathered if a male belonged to more than one rank class over the course
236 of the study. Finally, we tested the relationship between rank class and body weight by means
237 of a Kruskal-Wallis test.

238

239 The mixed model was calculated in SPSS 16 and all other tests were performed in R
240 2.7.0 (R Development Core Team 2008). All statistical tests were two-tailed with alpha set at
241 0.05. Where necessary, we corrected for multiple testing after Benjamini and Hochberg
242 (1995).

243

244 **RESULTS**

245 Throughout the study, only males gave loud calls and all adult males of both study
246 groups called regularly. **Loud calls were uttered to varying extents in the different**
247 **contexts (aggression: 45.3%; feeding: 25.6%; resting: 10.2%; moving: 6.6%; social**
248 **positive: 5.0%; mating: 3.9%; others, e.g. environmental stimuli: 3.3%; $N = 1769$ calls**
249 **from 23 males). They** were short (mean \pm SE = 0.418 \pm 0.094 s, $N = 194$), pulsed
250 vocalisations made up of two to nine distinct elements (Figure 1). From our observations it
251 seemed that single elements were produced during exhalation. The main acoustic energy of
252 single elements were distributed in two different frequency ranges, consisting of one small

253 low frequency band (DFB) between 0.7 and 1.2 kHz and higher frequency band with a
254 broader distribution of frequency energy between 2 and 8 kHz (DFA3, Fig. 1).

255

256 The mixed linear model revealed several significant differences related to rank but no
257 significant differences related to context (Table 3). High ranking males produced loud calls
258 containing more elements than middle and low ranking males (Figure 2a). In addition, call
259 elements of high ranking males showed a significant higher frequency in their second broader
260 frequency band than middle and low ranking males (Figure 2b). However, high and middle
261 ranking males did not differ in their low **frequency band, and only** low ranking males
262 produced DFB's with a higher frequency (Figure 2c).

263

264 In addition to rank related differences, the mixed linear model revealed significant
265 individual differences in the acoustic structure of call elements. A subsequent discriminant
266 function analysis including all acoustic parameters resulted in a correct assignment of 87.6%
267 of all cases (leave-one-out cross validation: 78.9%).

268

269 A Kruskal-Wallis test revealed significant differences in calling rate between rank
270 classes ($\chi^2_2 = 9.156, P = 0.010$), with high ranking males calling more often than middle and
271 low ranking males (Figure 2d). Particularly alpha males called at high rates and gave on
272 average 3.0 loud calls per hour (range: 2.2 – 3.8, $N = 3$).

273

274 Males weighed on average 11.2 kg (range 9.5 – 12.7 kg). We did not find significant
275 correlations between body weight and any of the seven acoustic parameters (Table 4) and
276 calling rate ($r_s = 0.285, N = 13, P = 0.345$). Furthermore, there were no significant differences
277 in body weight between rank classes (Kruskal-Wallis test: $\chi^2_2 = 1.242, P = 0.537$).

278

279

280 **DISCUSSION**

281 Our present results suggest that loud calls uttered during different contexts can be considered
282 as one call type, since we did not find any significant structural differences between these
283 calls. Furthermore, loud calls fulfilled both criteria for sexually selected traits proposed by
284 Snowdon (2004) and tested in this study: i) they were only uttered by males (and are thus
285 sexually dimorphic) and ii) it seems possible to identify individuals through their acoustic
286 display of dominance. The acoustic structure furthermore encoded the caller's dominance
287 rank (independent of male identity and vice versa), which was also reflected in the number of
288 emitted loud calls, with alpha- and beta-males calling most often. This provides the first direct
289 evidence for a display of dominance in a tolerant primate species.

290

291 Since the acoustic structure of loud calls uttered in different contexts has never been
292 investigated in crested macaques, we first clarified whether call structure is affected by the
293 context of calling. Surprisingly, we found no indication for contextual differences in loud call
294 structure although contexts varied significantly concerning **social context (e.g. mating vs.**
295 **aggression)**. **Apparently, in crested macaques, loud calls can not be used to identify the**
296 **specific context they are given in.** They can, however, potentially be used to identify the
297 caller's dominance rank and thus his competitive ability. A similar finding has been made in
298 chacma baboons, where loud calls also encode information about male dominance rank and
299 fighting ability (Kitchen et al. 2003; Fischer et al. 2004). Here, the frequency with which loud
300 calls are uttered has been interpreted to signal male quality in terms of the ability to carry
301 energetic costs (Fischer et al. 2004, see also Taigen & Wells 1985; Eberhardt 1994).
302 Signalling quality to others is usually seen as part of a sexually selected trait (Vehrencamp
303 2000).

304

305 In crested macaques, male dominance status is not only reflected in the frequency with
306 which males call, but also in call structure. High-ranking males produced lower dominant
307 frequency bands (DFBs) and more energy in high frequencies (i.e. higher DFA3s) than low-
308 ranking males. These parameters seem to carry no obvious costs, but may instead reflect a
309 certain physiological quality of the calling male, for example body size. According to Morton
310 (1977), low fundamental frequencies (the correspondent of DFBs in non-tonal calls
311 [Hammerschmidt & Jürgens 2007]) are linked to large body size, because low frequencies can
312 only be produced by large individuals. Assuming that bigger animals also have greater
313 fighting ability, the DFB should be a good indicator of dominance rank. With the exception of
314 toads and frogs, this hypothesis has however received little support so far - firstly because
315 dominance is usually not only affected by body size but seems to be a multi-factorial
316 phenomenon in most animal taxa (e.g. Missakian 1972; Dingemanse & de Goede 2004), and
317 secondly because fundamental frequency is only weakly correlated with body size in most
318 vertebrates including primates (McComb 1991; Fitch 1997, but see Pfefferle & Fischer 2006).
319 It is therefore surprising that crested macaque loud calls appear to fit the predictions set up by
320 Morton, especially considering we did not find any significant correlation between male body
321 weight and dominance rank or body weight and any of the call parameters in this species.
322 Body weight thus seems to be a poor indicator of male fighting ability in this species and does
323 also not affect loud call characteristics. It may, however, be that body weight does not
324 represent body size in male crested macaques. Further investigations directly measuring body
325 size may thus be more useful to test Morton's predictions in this species. On the other hand,
326 loud calls did not only encode male dominance rank through low frequencies. Together with
327 lower DFBs, high-ranking males also produced higher pitched calls, i.e. calls with higher
328 DFA3. This finding again contradicts Morton's predictions (1977), since high rank in crested
329 macaques is encoded by both, low and high frequencies supporting the finding that Morton's
330 hypothesis does not consistently apply to primates. Why dominance rank is reflected in both

331 extremes and in how far spectral parameters of loud calls represent male quality other than
332 mere competitive ability in crested macaques (e.g. MHC) needs further investigation.

333

334 Another striking difference between chacma baboon and crested macaque loud calls is
335 that in baboons, loud calls are in the majority of cases given by contesting males (Kitchen et
336 al. 2003). In crested macaques, however, these calls are given mainly by bystanders rather
337 than contesters even when they occur within the context of aggression. Whereas in baboons
338 loud calls thus seem to serve prevention of contest escalation, crested macaques may use loud
339 calls to avoid contest in the first place. This conclusion is also supported by the observation
340 that loud calls are not only uttered during aggression, but also during other contexts.
341 However, further investigation into the effect of loud calls on the frequency of male contest is
342 needed to further clarify the role of loud calls for male-male competition.

343

344 The observation that loud calls in crested macaques are only uttered by males while
345 females of this species lack such a formal signal supports the hypothesis that in so called
346 tolerant primate species (i.e. grade 4 species: Thierry 2000), status indicators should prevent
347 contest and thus only occur if power is asymmetrically distributed over group members
348 (Preuschoft & van Schaik 2000; Thierry 2004). **Female crested macaques are thought to**
349 **experience only weak competition over resources and thus power asymmetries between**
350 **females are small.** A status indicator preventing contest seems therefore unnecessary for
351 them (Preuschoft & van Schaik 2000). Males, on the other hand, compete for fertile females –
352 a resource that cannot be shared – with high-ranking males monopolising access to females
353 (Rohr 2008), meaning that power is asymmetrically distributed among males (see also Reed et
354 al. 1997). Hence, a divergence exists in the degree of intra-sexual competition between the
355 sexes, which may explain the **occurrence** of a male specific signal of dominance, not only in
356 crested macaques, but possibly also in other species with loud calls. In despotic species, in

357 contrast, both sexes seem to face similar pressures of competition (though from different
358 sources), which is thought to be the reason for the occurrence of status indicators in both
359 sexes (Preuschoft & van Schaik 2000). Given the presence of a status indicator, male specific
360 indicators should not be necessary and therefore not occur in despotic species. This line of
361 argument may partly explain why loud calls occur only in some primate species and why they
362 do not occur, for example, in pig-tailed macaques (*M. nemestrina*), the only macaque species
363 of the silenus-group that is classified as despotic and the only one without male loud calls. In
364 order to better understand the evolution of primate status indicators, it will be useful to
365 investigate whether male signals of dominance occur only in those species in which male-
366 male competition for females strongly outweighs female-female competition for resources.

367

368 Taken together, the results of this study for the first time present evidence for a signal
369 of dominance in a tolerant macaque species, the signal however being restricted to males. Our
370 study therefore demonstrates the importance of the differentiation between male and female
371 competition types when investigating primate social and communication styles. Furthermore,
372 the finding that loud calls are sexually dimorphic and signal individual rank and thus fighting
373 ability in crested macaques, suggests that these vocalisations represent a sexually selected trait
374 in this species, possibly serving to prevent contest between males. Theoretical considerations
375 concerning the evolution of status indicators in primates support this hypothesis. Our study
376 thus sets the basis for more detailed studies aiming at finally clarifying whether loud calls in
377 crested macaques represent a sexual signal, whether they **are subject to** pressures of intra-
378 sexual selection and in how far they also serve to attract females. **A question that also still**
379 **remains open is whether loud calls originally developed under the pressures of sexual**
380 **selection in this species or whether they underwent a functional change over time.** Using
381 more detailed behavioural observations in combination with playback experiments, we now
382 intend to further examine criteria ascribed to sexual signals (Snowdon 2004), investigating to

383 what extent loud calls occur in the context of reproduction, how they affect male contest,
384 whether they attract females and in how far their properties correlate with male reproductive
385 success.

386

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401

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557

558 **Figures' legends:**

559

560 **Figure 1:** Spectrogram of a crested macaque loud call, illustrating some of the acoustic
561 parameters, i.e. the low frequency band (DFB) and high frequency band (measured as DFA3,
562 see table 2) and the number of distinct call elements.

563

564 **Figure 2:** Dominance related differences in acoustic structure and calling rate of male loud
565 calls (mean and standard error).

566

567 **Table 1.** Group membership, observation time, number of loud call recordings and dominance
 568 rank class of the study males. For males marked with an asterisk body weights were obtained.

Male	Group	Observation time [h]	Recorded loud calls	Rank class
BJ*	R2	162.1	16	high, middle
CJ*	R2	166.5	5	middle, low
DJ	R1	158.3	5	middle, low
EJ*	R1	155.1	5	high
FJ*	R1	153.8	26	high
GM*	R2	21.7		middle
HJ*	R2	10.8		high
IJ	R1	170.9	43	high
JJ	R1	147.4		low, middle
KJ*	R2	164.2	4	high, middle, low
LJ	R1	39.3		low, middle
MJ	R1	161.2	7	middle
NJ*	R1	82.5	3	low, middle
OJ*	R1	157.0	2	low
PJ	R2	133.3	9	low
QJ	R2	31.5		middle
RJ*	R2	168.7	5	low, middle
SJ	R2	93.2	28	high
TJ*	R2	82.7		low, middle
VJ*	R2	87.1		low, middle, high
XJ	R1	155.4	2	low
YJ	R2	87.7		high

ZJ*	R1/R2 ¹⁾	153.1	34	middle, high
<hr/>				
Total		2743.5	194	

¹⁾ ZJ migrated from R1 to R2 during the study and replaced SJ as alpha-male in R2.

569

570

571 **Table 2. Description of acoustic parameters.** All values for spectral parameters were
 572 averaged over all time segments of an entire call and obtained from LMA 8.4 (developed by
 573 K. Hammerschmidt). For a detailed description of the spectral parameter estimation see
 574 Schrader and Hammerschmidt (1997).

Acoustic parameter	Description
Temporal	
Number of elements	Number of distinct units making up the call
Mean element duration [s]	Average duration of the elements in a call
Delivery rate [elements / s]	Rate of delivery (elements produced per second)
Spectral	
DFA3 [kHz]	DFA3 is calculated by determining the frequency amplitudes across the spectrum for each time segment (in this study every 1.45 ms). From these values, the frequency was calculated at which the DFA reached the third quartile (75%) of the total distribution.
DFB [kHz]	DFB is characterized by amplitudes that exceed a given threshold (sum of means plus one standard deviation) as calculated from the adjacent frequency bins. In tonal calls the (lowest) DFB corresponds to the fundamental frequency.
Peak frequency [kHz]	Peak frequency is the frequency in each time segment of the spectrogram that has the greatest amplitude value, i.e. the most acoustic energy.
Frequency range [kHz]	Frequency range characterises the bandwidth with the main acoustic energy per time segment. The frequency range marks the first time the frequency amplitude exceeds a dynamic

threshold until the last time the frequency amplitude falls below
this threshold.

575
576

577 **Table 3:** Rank and context related differences in acoustic structure of loud calls of male
 578 crested macaques. Significant differences after Hochberg correction are marked by bold
 579 values.

Acoustic Parameter	Rank		Context	
	<i>F</i> values	<i>P</i>	<i>F</i> values	<i>P</i>
Number of elements	4.74	0.019	0.31	0.910
Mean element duration	0.97	0.385	1.28	0.272
Delivery rate	1.32	0.272	0.81	0.541
DFA3	5.22	0.007	3.25	0.008
DFB	6.07	0.006	1.20	0.313
Peak frequency	1.72	0.190	0.37	0.871
Frequency range	0.49	0.616	1.68	0.142

580

581

582 **Table 4:** Relationship between acoustic parameters and body weight.

Parameter	Correlation with weight	
	(N = 9 males)	
	<i>r_s</i>	<i>P</i>
Number of elements	-0.199	0.607
Mean element duration	0.345	0.363
Delivery rate	-0.067	0.864
DFA3	0.075	0.847
DFB	-0.508	0.162
Peak frequency	-0.444	0.232
Frequency range	-0.059	0.881

583

584

1 **Loud calls in male crested macaques (*Macaca nigra*)**

2 **– a signal of dominance in a tolerant species**

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5
6 **Running headline:** NEUMANN ET AL.: LOUD CALLS IN CRESTED MACAQUES

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25 Word count: 4264

26

27 Abstract:

28 Compared to other mammals, sexual signals occur particularly often within the primate order.
29 Nevertheless, little is known so far about the pressures under which these signals evolved. We
30 studied loud calls in wild crested macaques (*Macaca nigra*) in order to examine whether these
31 are used as a sexual signal, particularly as a signal of dominance in this species. Since the
32 structure of loud calls may be influenced by the context in which they are uttered, we tested
33 for contextual differences in call structure. Only males uttered loud calls and analysis of 194
34 loud calls given from 15 males showed that call structure encoded the caller's identity as well
35 as his social status. Dominance rank was also reflected in the frequency with which males
36 called with alpha males calling most often. The structure of loud calls was however not
37 influenced by context. Our findings consolidate the assumption that in crested macaques, loud
38 calls serve as a signal of dominance most likely used to prevent contest between males for
39 mates. We herewith provide the first direct evidence for a signal of dominance in a tolerant
40 primate species and discuss more in detail why this signal occurs only in one sex.

41

42 Key words: crested macaque, dominance signal, loud calls, *Macaca nigra*, sexual selection,
43 sexual signal, social style

44

45 The diversity of sexual signals occurring within the primate order intrigued Darwin (1876)
46 and is unique among mammals (e.g. Nunn 1999; Bradley & Mundy 2008). An acoustic signal
47 used in a variety of primate species that seems to function as a sexual signal at least in some
48 primate species is the loud call (synonymously called ‘long or long distance call’; Wich &
49 Nunn 2002). These vocalisations consist of loud, repetitive units and are usually uttered by
50 males (Gautier & Gautier 1977; Waser 1982; Mitani & Stuht 1998; Wich & Nunn 2002).
51 Although common in primates, the function of loud calls remains poorly understood.

52

53 From studies on other animal taxa, such as anurans, birds and ungulates, it is well
54 known that male acoustic signals play a role in male-male competition for mates (intra-sexual
55 selection) by signalling competitive abilities to contesters (e.g. Blanchard's cricket frog, *Acris*
56 *crepitans blanchardi*: Wagner 1992; red deer, *Cervus elaphus*: Reby et al. 2005) as well as in
57 attracting females (inter-sexual selection) by signalling individual quality to them (e.g. red
58 deer, *Cervus elaphus*: McComb 1991; gray tree frog, *Hyla versicolor*: Gerhardt et al. 2000;
59 red grouse, *Lagopus lagopus scoticus*: Mougeot et al. 2004).

60

61 For primates, in contrast, it has for a long time been assumed that loud calls have not
62 evolved through pressures of sexual selection, but are primarily used to mediate inter-group
63 spacing and intra-group cohesion (e.g. Riley 2005; da Cunha & Byrne 2006). Results of a
64 recent meta-analysis over the entire primate order however reveal that loud calls originally
65 served to defend resources and to attract mates (Wich & Nunn 2002), and thus presumably
66 still function in intra- and/or intersexual communication in a reproductive context. Although
67 direct evidence for this hypothesis is still missing, the few existing studies on the function of
68 loud calls lead to the conclusion that at least in some species, they represent a sexually
69 selected trait. In male chacma baboons (*Papio cynocephalus ursinus*) for example, loud calls
70 (‘wahoos’) signal dominance (Kitchen et al. 2003; Fischer et al. 2004) and play a role in male

71 agonistic interactions, e.g. during male-male chases, suggesting that wahoos serve a function
72 in male-male competition. In white-handed gibbons (*Hylobates lar*) and Thomas langurs
73 (*Presbytis thomasi*), loud calls signal a males pairing status (Raemaekers et al. 1984;
74 Reichard & Neumann 2007) and the life-phase he is in (see Steenbeek et al. 1999; Wich et al.
75 2003 for definition), respectively, suggesting that here, loud calls serve to attract females (but
76 see Mitani 1988) and in orangutans, male loud calls may serve both, male-male competition
77 and mate attraction (Delgado 2006). Apart from these studies, little is known about the
78 information content and potential function of these vocalisations and more studies are clearly
79 needed in order to better understand the adaptive significance of this trait in primates.

80

81 Crested macaques (*Macaca nigra*) are particularly interesting in this respect, since
82 they represent one of the few macaque species in which males utter loud calls (Wich & Nunn
83 2002). All macaque species share the same social system, living in multi-male multi-female,
84 female philopatric groups, but within the macaque genus, only species of the so called
85 silenus-lineage (with the exception of *Macaca nemestrina*, and *Macaca leonina*) exhibit loud
86 calls (Delson 1980; Tosi et al. 2003) raising the question why loud calls exist in these, but not
87 in other macaques. In addition, crested macaques seem to be the only calling macaque species
88 in which all adult males regularly vocalise whereas in the other macaques, calling is mainly
89 limited to alpha males (Baker et al. 1991; Okamoto 2001; Riley 2005). So far, macaque loud
90 calls have been interpreted to serve a function for inter-group spacing (Okamoto 2001),
91 within-group coordination (Riley 2005), species recognition (Muroyama & Thierry 1998)
92 and/or third party aggression intervention (Kinnaird & O'Brien 1999), but no study ever
93 examined the possibility that loud calls in Sulawesi macaques are subject to the pressures of
94 sexual selection.

95

96 Loud calls of crested macaques are also very interesting in a different context.
97 According to Thierry (2000, 2007), macaque species vary along a gradient of social styles,
98 mapped on a four-grade scale ranging from despotic to tolerant systems with crested
99 macaques belonging to the tolerant species (grade 4). Theoretical considerations led to the
100 predictions that despotic primate species should evolve signals of submission (i.e. low-
101 ranking individuals showing their subordination to higher-ranking ones) whereas tolerant
102 species should evolve signals of dominance (i.e. higher ranking individuals showing their
103 status to lower ranking individuals) or no status indicator, depending on the level of
104 asymmetry in dyadic conflicts and overall aggression intensity (Preuschoft & van Schaik
105 2000; Thierry 2004). Although there is ample evidence for signals of submission in despotic
106 (grades 1-2) and for signals of dominance in slightly tolerant macaques (grade 3; de Waal &
107 Luttrell 1985; Chaffin et al. 1995; Preuschoft 1995), there is to date no evidence for the
108 occurrence of dominance signals in any of the tolerant macaque (grade 4) species. Since
109 crested macaques belong to the group of tolerant macaques (Thierry 2000), it is particularly
110 interesting to investigate whether loud calls represent such a signal of dominance.

111
112 The aim of our study therefore was to investigate the information content of loud calls
113 in crested macaques in the light of two concepts: sexual selection theory and macaque social
114 style theory. Since crested macaques utter loud calls in different contexts (Kinnaird & O'Brien
115 1999) and the acoustic structure of these calls (and thus their information content and
116 function) may vary with context (like in chacma baboons; Fischer et al. 2002), we first
117 examined whether call structure varies in a context dependent manner. In a second step, we
118 investigated whether loud calls meet two major criteria for sexually selected signals, i.e.
119 whether the signal's expression is sexually dimorphic and whether there is variation in the
120 signal that can be assigned to individuals (Snowdon 2004). Furthermore, in order to
121 investigate whether loud calls signal male dominance, we examined the relationship between

122 the frequency of loud call utterance to selected acoustic call parameters and male dominance
123 rank. As a potential measure of male fighting ability and quality, the relationship between
124 male body weight, dominance rank and loud call characteristics were also examined. The
125 study was carried out on two wild groups of crested macaques living in the Tangkoko-
126 Batuangus Nature Reserve, North Sulawesi, Indonesia over a period of 14 months.

127

128

129 **METHODS**

130 **Study Site and Animals**

131 Data were collected on two groups of free ranging, wild crested macaques from July
132 2006 until August 2007 in the Tangkoko-Batuangus Nature Reserve, North Sulawesi,
133 Indonesia (1°33' N, 125°10' E). The reserve comprises an area of 8,867 ha lowland rainforest,
134 and ranges from sea level to 1,350 m (Collins et al. 1991; Rosenbaum et al. 1998). Two multi-
135 male groups ('R1' and 'R2') comprised 65-75 individuals each, including 7-10 and 9-10 adult
136 males, respectively. The ranging area of the study groups included undisturbed primary forest
137 as well as large areas of secondary forest and regenerating gardens with a severely damaged
138 canopy cover. The observed groups have been studied intermittently for more than ten years
139 (O'Brien & Kinnaird 1997; Reed et al. 1997; Kinnaird & O'Brien 1999) and were completely
140 habituated to human observers.

141

142 **Behavioural Data Collection**

143 We collected behavioural data on 23 males from the two groups using focal animal
144 sampling (Martin & Bateson 1993), resulting in 2743.5 hours of focal observation time (mean
145 focal hours per male: 119.3, range: 10.8 – 170.9, Table 1). Each male was followed once a
146 week, alternating from the male's descent from the sleeping tree until noon and from noon to
147 the time the focal male entered the sleeping tree. We used instantaneous sampling (Martin &

148 Bateson 1993) with a time interval of one minute for the focal animal's activity, noting the
149 occurrence of loud calls, social interactions (socio-positive and agonistic behaviour, mating)
150 and displacement interactions between males as continuous events. Agonistic and
151 displacement interactions between males were furthermore recorded ad libitum.

152

153 **Dominance Rank**

154 For rank allocation, we divided the study period into six distinct time periods, since group
155 composition varied over the course of the study due to migration events and maturation of
156 subadult males. Periods ranged from 49 to 92 days. During each period and for each group
157 separately, we created matrices containing dyadic dominance interactions (agonistic
158 interactions with unambiguous winner and loser, and displacement interactions (Thierry et al.
159 2000) for all adult males present during the given period. Only conflicts were taken into
160 account that did not include counter aggression by the 'victim/loser', i.e. only unidirectional
161 interactions.

162

163 We then tested whether it was justified to rank males linearly by means of de Vries'
164 (1995) h' index. The linearity indices have an average value of 0.72 (range: 0.53 – 0.94) and
165 the average p-value indicating whether linearity is different from what is expected by chance
166 is $p = 0.028$ (maximum $p = 0.069$). Even though 3 out of 12 hierarchies did not reach
167 statistical significance, we ranked males according to the I&SI method (de Vries 1998), with
168 rank 1 being the highest rank. Three hierarchies were found to contain inconsistencies, i.e. the
169 dyadic relationship between two males was reversed in the ordering produced by the
170 algorithm. Although in the two cases for which we have data, the inconsistencies predicted
171 the order in the subsequent time period, we created three rank classes: high (ranks 1 – 3),
172 middle (ranks 4 – 6) and low (ranks 7 – 10).

173

174 **Body Weight**

175 We weighed adult males. For this, a digital scale (modified Combics scale, Sartorius,
176 Göttingen, Germany, weight step = 0.02 kg) was positioned at a fixed location and single
177 males were lured onto the scale with a small amount of corn when a group was passing the
178 scale's position. Reading of the scale took place via a remote display. Measures were only
179 taken into account if a male was weighed at least twice during one weighing session.

180

181 **Vocal Recording & Acoustic Analysis**

182 Loud calls were recorded ad-libitum and the context in which the call occurred was
183 noted. Recordings were done with a digital portable solid state recorder (PMD660, Marantz,
184 Itasca, Illinois) and a directional microphone (K6-ME66, Sennheiser, Wedemark, Germany)
185 equipped with a windshield (265E, Rycote, Gloucestershire, UK) at a sampling rate of 44.1
186 kHz. We recorded a total of 194 loud calls of sufficient quality for analysis from six contexts:

- 187 • aggression = calls given during or immediately after an aggressive interaction, $N = 40$
188 • resting = calls given outside any obvious context, i.e. during resting periods, $N = 57$
189 • feeding = calls given during feeding or foraging activity, $N = 8$
190 • moving = calls given during group movement, $N = 13$
191 • social positive = calls that occurred in or followed affiliative interactions, such as
192 grooming, male-male mounting, genital grasp, $N = 12$
193 • mating = calls emitted during or shortly after copulation, $N = 64$

194

195 All calls were first inspected visually using SASLab Pro 4.39 (Avisoft Bioacoustics,
196 Berlin, Germany) to make sure that background noises (e.g. bird song and other individuals
197 calling) were not present in the recordings. The spectrogram settings that were applied for the
198 extraction were: FFT length = 1024 points, window = Hamming, frame size = 100%, overlap
199 = 96.87%. The resulting frequency resolution was 43 Hz at a time increment of 0.73 ms. After

200 down sampling the recordings to 22.05 kHz, frequency resolution was 22 Hz at a time
201 increment of 1.45 ms. All parameters were taken from down-sampled recordings, except
202 frequency range for which the original sampling rate was kept. For one parameter (dominant
203 frequency band), we applied a band pass filter to limit the frequency range of the signal, in
204 order to measure the band between 0.7 and 1.5 kHz ($f_{\text{high}} = 0.3$ kHz, $f_{\text{low}} = 2$ kHz, see Figure
205 1). All spectrograms were saved as ASCII files for further processing. We then measured
206 seven acoustic parameters: three temporal and four frequency parameters, which were suited
207 to describe structural variations in loud calls (for detailed description see Fig. 1 and Table 2).

208

209 **Statistical Analysis**

210 We determined the general frequency with which loud calls were uttered in the
211 different contexts by first calculating the percentages with which each male called in the
212 different contexts (i.e. 100% = all calls of a single male) and subsequently calculating the
213 mean percentage over all males for each context.

214

215 We conducted a mixed linear model to evaluate structural differences in male loud
216 calls related to rank and context. We used rank class and context as fixed factors and caller
217 identity and study group as random factor, and calculated tests for all seven acoustic
218 parameters. As study group did not improve our models, we excluded this factor from the
219 final models.

220

221 To describe individual differences in the structure of loud calls we conducted a
222 discriminant function analysis including all acoustic parameters. To validate the original
223 classification results of this analysis, we performed a cross validation using the leave-one-out
224 method. This method classifies each case based on functions derived by all but the one case.

225

226 To investigate the relation between call structure and body weight, we used
227 Spearman's rank correlation. For this, we calculated mean parameter values of all calls of a
228 given male while belonging to one rank class and used these means to correlate them with
229 body weight.

230

231 For each male, the mean frequency of call utterance (loud calls/hour) was calculated
232 and the influence of dominance rank class on this parameter was tested with a Kruskal-Wallis
233 test. To control for potential rank effects, we used data from the rank class for which most
234 observation time was gathered if a male belonged to more than one rank class over the course
235 of the study. Finally, we tested the relationship between rank class and body weight by means
236 of a Kruskal-Wallis test.

237

238 The mixed model was calculated in SPSS 16 and all other tests were performed in R
239 2.7.0 (R Development Core Team 2008). All statistical tests were two-tailed with alpha set at
240 0.05. Where necessary, we corrected for multiple testing after Benjamini and Hochberg
241 (1995).

242

243 **RESULTS**

244 Throughout the study, only males gave loud calls and all adult males of both study
245 groups called regularly. Loud calls were uttered to varying extents in the different contexts
246 (aggression: 45.3%; feeding: 25.6%; resting: 10.2%; moving: 6.6%; social positive: 5.0%;
247 mating: 3.9%; others, e.g. environmental stimuli: 3.3%; $N = 1769$ calls from 23 males). They
248 were short (mean \pm SE = 0.418 ± 0.094 s, $N = 194$), pulsed vocalisations made up of two to
249 nine distinct elements (Figure 1). From our observations it seemed that single elements were
250 produced during exhalation. The main acoustic energy of single elements were distributed in
251 two different frequency ranges, consisting of one small low frequency band (DFB) between

252 0.7 and 1.2 kHz and higher frequency band with a broader distribution of frequency energy
253 between 2 and 8 kHz (DFA3, Fig. 1).

254

255 The mixed linear model revealed several significant differences related to rank but no
256 significant differences related to context (Table 3). High ranking males produced loud calls
257 containing more elements than middle and low ranking males (Figure 2a). In addition, call
258 elements of high ranking males showed a significant higher frequency in their second broader
259 frequency band than middle and low ranking males (Figure 2b). However, high and middle
260 ranking males did not differ in their low frequency band, and only low ranking males
261 produced DFB's with a higher frequency (Figure 2c).

262

263 In addition to rank related differences, the mixed linear model revealed significant
264 individual differences in the acoustic structure of call elements. A subsequent discriminant
265 function analysis including all acoustic parameters resulted in a correct assignment of 87.6%
266 of all cases (leave-one-out cross validation: 78.9%).

267

268 A Kruskal-Wallis test revealed significant differences in calling rate between rank
269 classes ($X^2_2 = 9.156$, $P = 0.010$), with high ranking males calling more often than middle and
270 low ranking males (Figure 2d). Particularly alpha males called at high rates and gave on
271 average 3.0 loud calls per hour (range: 2.2 – 3.8, $N = 3$).

272

273 Males weighed on average 11.2 kg (range 9.5 – 12.7 kg). We did not find significant
274 correlations between body weight and any of the seven acoustic parameters (Table 4) and
275 calling rate ($r_s = 0.285$, $N = 13$, $P = 0.345$). Furthermore, there were no significant differences
276 in body weight between rank classes (Kruskal-Wallis test: $X^2_2 = 1.242$, $P = 0.537$).

277

278

279 **DISCUSSION**

280 Our present results suggest that loud calls uttered during different contexts can be considered
281 as one call type, since we did not find any significant structural differences between these
282 calls. Furthermore, loud calls fulfilled both criteria for sexually selected traits proposed by
283 Snowdon (2004) and tested in this study: i) they were only uttered by males (and are thus
284 sexually dimorphic) and ii) it seems possible to identify individuals through their acoustic
285 display of dominance. The acoustic structure furthermore encoded the caller's dominance
286 rank (independent of male identity and vice versa), which was also reflected in the number of
287 emitted loud calls, with alpha- and beta-males calling most often. This provides the first direct
288 evidence for a display of dominance in a tolerant primate species.

289

290 Since the acoustic structure of loud calls uttered in different contexts has never been
291 investigated in crested macaques, we first clarified whether call structure is affected by the
292 context of calling. Surprisingly, we found no indication for contextual differences in loud call
293 structure although contexts varied significantly concerning social context (e.g. mating vs.
294 aggression). Apparently, in crested macaques, loud calls can not be used to identify the
295 specific context they are given in. They can, however, potentially be used to identify the
296 caller's dominance rank and thus his competitive ability. A similar finding has been made in
297 chacma baboons, where loud calls also encode information about male dominance rank and
298 fighting ability (Kitchen et al. 2003; Fischer et al. 2004). Here, the frequency with which loud
299 calls are uttered has been interpreted to signal male quality in terms of the ability to carry
300 energetic costs (Fischer et al. 2004, see also Taigen & Wells 1985; Eberhardt 1994).
301 Signalling quality to others is usually seen as part of a sexually selected trait (Vehrencamp
302 2000).

303

304 In crested macaques, male dominance status is not only reflected in the frequency with
305 which males call, but also in call structure. High-ranking males produced lower dominant
306 frequency bands (DFBs) and more energy in high frequencies (i.e. higher DFA3s) than low-
307 ranking males. These parameters seem to carry no obvious costs, but may instead reflect a
308 certain physiological quality of the calling male, for example body size. According to Morton
309 (1977), low fundamental frequencies (the correspondent of DFBs in non-tonal calls
310 [Hammerschmidt & Jürgens 2007]) are linked to large body size, because low frequencies can
311 only be produced by large individuals. Assuming that bigger animals also have greater
312 fighting ability, the DFB should be a good indicator of dominance rank. With the exception of
313 toads and frogs, this hypothesis has however received little support so far - firstly because
314 dominance is usually not only affected by body size but seems to be a multi-factorial
315 phenomenon in most animal taxa (e.g. Missakian 1972; Dingemanse & de Goede 2004), and
316 secondly because fundamental frequency is only weakly correlated with body size in most
317 vertebrates including primates (McComb 1991; Fitch 1997, but see Pfefferle & Fischer 2006).
318 It is therefore surprising that crested macaque loud calls appear to fit the predictions set up by
319 Morton, especially considering we did not find any significant correlation between male body
320 weight and dominance rank or body weight and any of the call parameters in this species.
321 Body weight thus seems to be a poor indicator of male fighting ability in this species and does
322 also not affect loud call characteristics. It may, however, be that body weight does not
323 represent body size in male crested macaques. Further investigations directly measuring body
324 size may thus be more useful to test Morton's predictions in this species. On the other hand,
325 loud calls did not only encode male dominance rank through low frequencies. Together with
326 lower DFBs, high-ranking males also produced higher pitched calls, i.e. calls with higher
327 DFA3. This finding again contradicts Morton's predictions (1977), since high rank in crested
328 macaques is encoded by both, low and high frequencies supporting the finding that Morton's
329 hypothesis does not consistently apply to primates. Why dominance rank is reflected in both

330 extremes and in how far spectral parameters of loud calls represent male quality other than
331 mere competitive ability in crested macaques (e.g. MHC) needs further investigation.

332

333 Another striking difference between chacma baboon and crested macaque loud calls is
334 that in baboons, loud calls are in the majority of cases given by contesting males (Kitchen et
335 al. 2003). In crested macaques, however, these calls are given mainly by bystanders rather
336 than contesters even when they occur within the context of aggression. Whereas in baboons
337 loud calls thus seem to serve prevention of contest escalation, crested macaques may use loud
338 calls to avoid contest in the first place. This conclusion is also supported by the observation
339 that loud calls are not only uttered during aggression, but also during other contexts.
340 However, further investigation into the effect of loud calls on the frequency of male contest is
341 needed to further clarify the role of loud calls for male-male competition.

342

343 The observation that loud calls in crested macaques are only uttered by males while
344 females of this species lack such a formal signal supports the hypothesis that in so called
345 tolerant primate species (i.e. grade 4 species: Thierry 2000), status indicators should prevent
346 contest and thus only occur if power is asymmetrically distributed over group members
347 (Preuschoft & van Schaik 2000; Thierry 2004). Female crested macaques are thought to
348 experience only weak competition over resources and thus power asymmetries between
349 females are small. A status indicator preventing contest seems therefore unnecessary for them
350 (Preuschoft & van Schaik 2000). Males, on the other hand, compete for fertile females – a
351 resource that cannot be shared – with high-ranking males monopolising access to females
352 (Rohr 2008), meaning that power is asymmetrically distributed among males (see also Reed et
353 al. 1997). Hence, a divergence exists in the degree of intra-sexual competition between the
354 sexes, which may explain the occurrence of a male specific signal of dominance, not only in
355 crested macaques, but possibly also in other species with loud calls. In despotic species, in

356 contrast, both sexes seem to face similar pressures of competition (though from different
357 sources), which is thought to be the reason for the occurrence of status indicators in both
358 sexes (Preuschoft & van Schaik 2000). Given the presence of a status indicator, male specific
359 indicators should not be necessary and therefore not occur in despotic species. This line of
360 argument may partly explain why loud calls occur only in some primate species and why they
361 do not occur, for example, in pig-tailed macaques (*M. nemestrina*), the only macaque species
362 of the silenus-group that is classified as despotic and the only one without male loud calls. In
363 order to better understand the evolution of primate status indicators, it will be useful to
364 investigate whether male signals of dominance occur only in those species in which male-
365 male competition for females strongly outweighs female-female competition for resources.

366

367 Taken together, the results of this study for the first time present evidence for a signal
368 of dominance in a tolerant macaque species, the signal however being restricted to males. Our
369 study therefore demonstrates the importance of the differentiation between male and female
370 competition types when investigating primate social and communication styles. Furthermore,
371 the finding that loud calls are sexually dimorphic and signal individual rank and thus fighting
372 ability in crested macaques, suggests that these vocalisations represent a sexually selected trait
373 in this species, possibly serving to prevent contest between males. Theoretical considerations
374 concerning the evolution of status indicators in primates support this hypothesis. Our study
375 thus sets the basis for more detailed studies aiming at finally clarifying whether loud calls in
376 crested macaques represent a sexual signal, whether they are subject to pressures of intra-
377 sexual selection and in how far they also serve to attract females. A question that also still
378 remains open is whether loud calls originally developed under the pressures of sexual
379 selection in this species or whether they underwent a functional change over time. Using more
380 detailed behavioural observations in combination with playback experiments, we now intend
381 to further examine criteria ascribed to sexual signals (Snowdon 2004), investigating to what

382 extent loud calls occur in the context of reproduction, how they affect male contest, whether
383 they attract females and in how far their properties correlate with male reproductive success.

384

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399

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556 **Figures' legends:**

557

558 **Figure 1:** Spectrogram of a crested macaque loud call, illustrating some of the acoustic
559 parameters, i.e. the low frequency band (DFB) and high frequency band (measured as DFA3,
560 see table 2) and the number of distinct call elements.

561

562 **Figure 2:** Dominance related differences in acoustic structure and calling rate of male loud
563 calls (mean and standard error).

564

565 **Table 1.** Group membership, observation time, number of loud call recordings and dominance
 566 rank class of the study males. For males marked with an asterisk body weights were obtained.

Male	Group	Observation time [h]	Recorded loud calls	Rank class
BJ*	R2	162.1	16	high, middle
CJ*	R2	166.5	5	middle, low
DJ	R1	158.3	5	middle, low
EJ*	R1	155.1	5	high
FJ*	R1	153.8	26	high
GM*	R2	21.7		middle
HJ*	R2	10.8		high
IJ	R1	170.9	43	high
JJ	R1	147.4		low, middle
KJ*	R2	164.2	4	high, middle, low
LJ	R1	39.3		low, middle
MJ	R1	161.2	7	middle
NJ*	R1	82.5	3	low, middle
OJ*	R1	157.0	2	low
PJ	R2	133.3	9	low
QJ	R2	31.5		middle
RJ*	R2	168.7	5	low, middle
SJ	R2	93.2	28	high
TJ*	R2	82.7		low, middle
VJ*	R2	87.1		low, middle, high
XJ	R1	155.4	2	low
YJ	R2	87.7		high

ZJ*	R1/R2 ¹⁾	153.1	34	middle, high
<hr/>				
Total		2743.5	194	

¹⁾ ZJ migrated from R1 to R2 during the study and replaced SJ as alpha-male in R2.

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568

569 **Table 2. Description of acoustic parameters.** All values for spectral parameters were
 570 averaged over all time segments of an entire call and obtained from LMA 8.4 (developed by
 571 K. Hammerschmidt). For a detailed description of the spectral parameter estimation see
 572 Schrader and Hammerschmidt (1997).

Acoustic parameter	Description
Temporal	
Number of elements	Number of distinct units making up the call
Mean element duration [s]	Average duration of the elements in a call
Delivery rate [elements / s]	Rate of delivery (elements produced per second)
Spectral	
DFA3 [kHz]	DFA3 is calculated by determining the frequency amplitudes across the spectrum for each time segment (in this study every 1.45 ms). From these values, the frequency was calculated at which the DFA reached the third quartile (75%) of the total distribution.
DFB [kHz]	DFB is characterized by amplitudes that exceed a given threshold (sum of means plus one standard deviation) as calculated from the adjacent frequency bins. In tonal calls the (lowest) DFB corresponds to the fundamental frequency.
Peak frequency [kHz]	Peak frequency is the frequency in each time segment of the spectrogram that has the greatest amplitude value, i.e. the most acoustic energy.
Frequency range [kHz]	Frequency range characterises the bandwidth with the main acoustic energy per time segment. The frequency range marks the first time the frequency amplitude exceeds a dynamic

threshold until the last time the frequency amplitude falls below
this threshold.

573
574

575 **Table 3:** Rank and context related differences in acoustic structure of loud calls of male
 576 crested macaques. Significant differences after Hochberg correction are marked by bold
 577 values.

Acoustic Parameter	Rank		Context	
	<i>F</i> values	<i>P</i>	<i>F</i> values	<i>P</i>
Number of elements	4.74	0.019	0.31	0.910
Mean element duration	0.97	0.385	1.28	0.272
Delivery rate	1.32	0.272	0.81	0.541
DFA3	5.22	0.007	3.25	0.008
DFB	6.07	0.006	1.20	0.313
Peak frequency	1.72	0.190	0.37	0.871
Frequency range	0.49	0.616	1.68	0.142

578

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580 **Table 4:** Relationship between acoustic parameters and body weight.

Parameter	Correlation with weight	
	(N = 9 males)	
	r_s	P
Number of elements	-0.199	0.607
Mean element duration	0.345	0.363
Delivery rate	-0.067	0.864
DFA3	0.075	0.847
DFB	-0.508	0.162
Peak frequency	-0.444	0.232
Frequency range	-0.059	0.881

581

582

Figure 1
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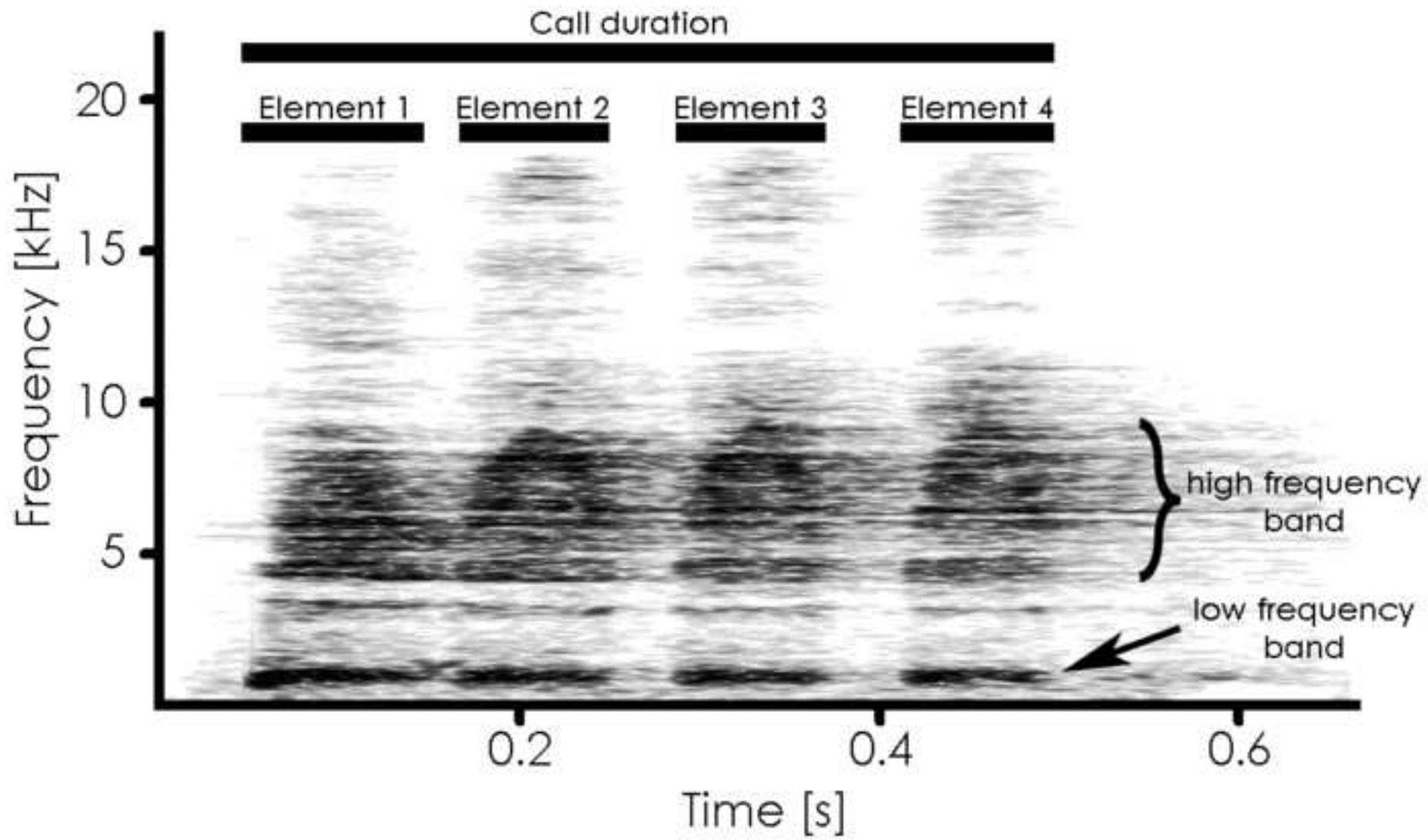
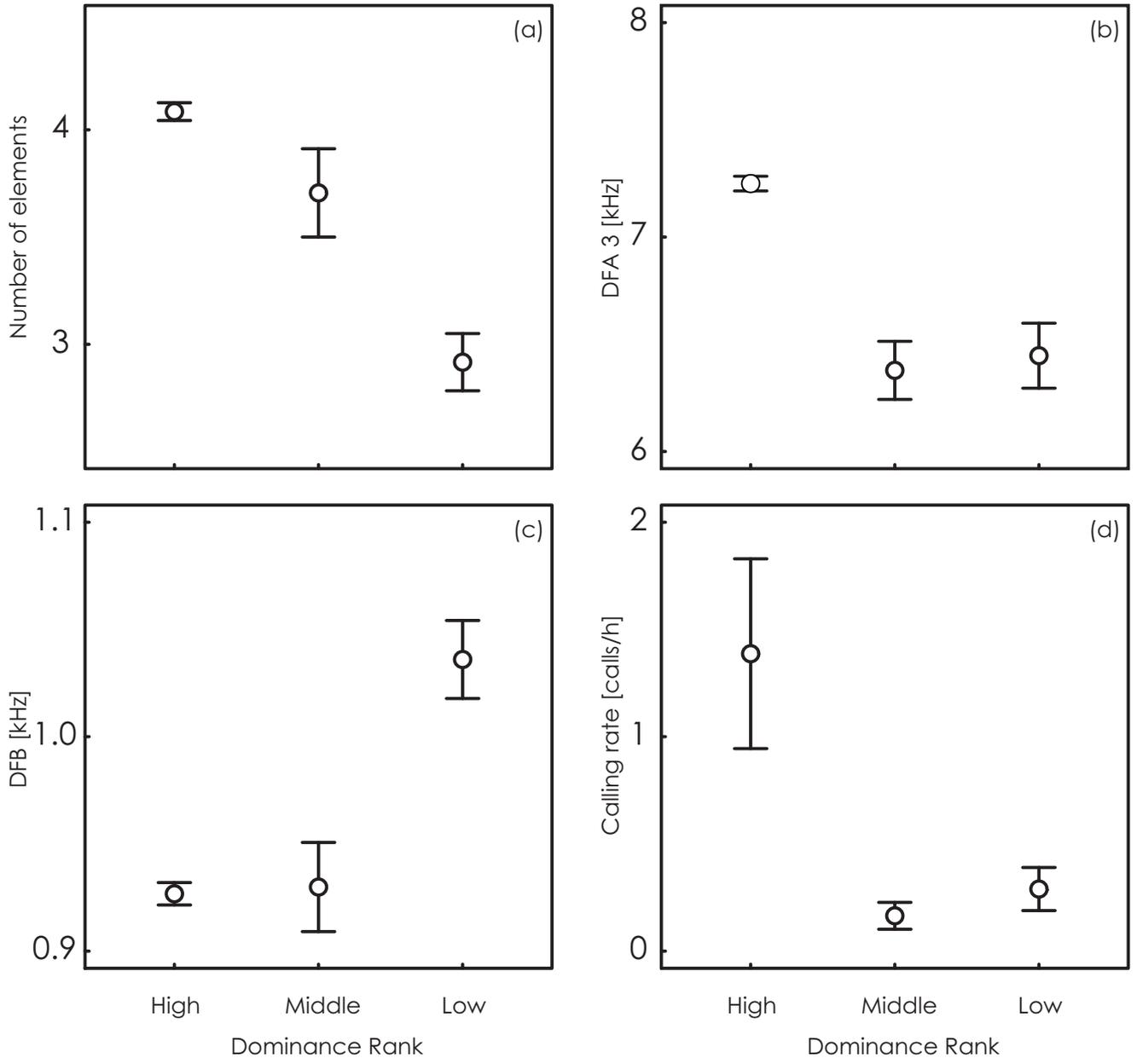


Figure 2



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Summary:

Crested macaques (*Macaca nigra*) are one of the few macaque species in which males utter loud calls. Since the information content and function of these calls still remains unclear, we conducted a detailed acoustic and behavioural analysis on calls uttered in a wild population. We found that loud calls encode male social status suggesting that they serve as signals of dominance to regulate competition for mates among males. Our finding provides the first hint to a signal of dominance in a macaque species with a so called tolerant social style. It also shows that males and females may differ in their use of status signals. Most likely female crested macaques do not need a signal of dominance because their social relationships are relaxed due to a low degree of female-female competition. We conclude that sex-specific differences in resource competition have to be taken into account when studying primate social and communication styles.