Neumann, C, Assahad, G, Hammerschmidt, K, Perwitasari-Farajallah, D and Engelhardt, A

Loud calls in male crested macaques, Macaca nigra: a signal of dominance in a tolerant species

http://researchonline.ljmu.ac.uk/id/eprint/3206/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Neumann, C, Assahad, G, Hammerschmidt, K, Perwitasari-Farajallah, D and Engelhardt, A (2010) Loud calls in male crested macaques, Macaca nigra: a signal of dominance in a tolerant species. Animal Behaviour, 79 (1). pp. 187-193. ISSN 0003-3472

Loud calls in male crested macaques (*Macaca nigra*) – a signal of dominance in a tolerant species

Christof Neumann[a,b], Gholib Assahad[c,d], Kurt Hammerschmidt[e],
Dyah Perwitasari-Farajallah[c,f], Antje Engelhardt[a,c,*]

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

[a] Department of Reproductive Biology, German Primate Centre, Göttingen, Germany
[b] Department of Animal Physiology, Faculty for Life Sciences, Pharmacy and Psychology, University Leipzig, Germany
[c] Primate Research Centre, Bogor Agricultural University, Indonesia
[d] Faculty of Veterinary Medicine, Bogor Agricultural University, Indonesia
[e] Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany
[f] Department of Biology, Faculty of Mathematics & Natural Sciences, Bogor Agricultural University, Indonesia

* Correspondence: Antje Engelhardt, Department of Reproductive Biology, Deutsches Primatenzentrum GmbH, Kellnerweg 4, 37077 Göttingen, Germany (email: aengelhardt@dpz.eu)

Word count: **4264**

Abstract:

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

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

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

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

For primates, in contrast, it has for a long time been assumed that loud calls have not evolved through pressures of sexual selection, but are primarily used to mediate inter-group spacing and intra-group cohesion (e.g. Riley 2005; da Cunha & Byrne 2006). Results of a recent meta-analysis over the entire primate order however reveal that loud calls originally served to defend resources and to attract mates (Wich & Nunn 2002), and thus presumably still function in intra- and/or intersexual communication in a reproductive context. Although direct evidence for this hypothesis is still missing, the few existing studies on the function of loud calls lead to the conclusion that at least in some species, they represent a sexually selected trait. In male chacma baboons (*Papio cynocephalus ursinus*) for example, loud calls (‘wahoos’) signal dominance (Kitchen et al. 2003; Fischer et al. 2004) and play a role in male agonistic interactions, e.g. during male-male chases, suggesting that wahoos serve a function in male-male competition. In white-handed gibbons (*Hylobates lar*) and Thomas langurs (*Presbytis thomasii*), loud calls signal a males pairing status (Raemaekers et al. 1984; Reichard & Neumann 2007) and the life-phase he is in (see Steenbeek et al. 1999; Wich et al. 2003 for definition), respectively, suggesting that here, loud calls serve to attract females (but see Mitani 1988) and in orangutans, male loud calls may serve both, male-male competition and mate attraction (Delgado 2006). Apart from these studies, little is known about the information content and potential function of these vocalisations and more studies are clearly needed in order to better understand the adaptive significance of this trait in primates.

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

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

The aim of our study therefore was to investigate the information content of loud calls in crested macaques in the light of two concepts: sexual selection theory and macaque social style theory. Since crested macaques utter loud calls in different contexts (Kinnaird & O'Brien 1999) and the acoustic structure of these calls (and thus their information content and function) may vary with context (like in chacma baboons; Fischer et al. 2002), we first examined whether call structure varies in a context dependent manner. In a second step, we investigated whether loud calls meet two major criteria for sexually selected signals, i.e. whether the signal’s expression is sexually dimorphic and whether there is variation in the signal that can be assigned to individuals (Snowdon 2004). Furthermore, in order to investigate whether loud calls signal male dominance, we examined the relationship between the frequency of loud call utterance to selected acoustic call parameters and male dominance rank. As a potential measure of male fighting ability and quality, the relationship between male body weight, dominance rank and loud call characteristics were also examined. The study was carried out on two wild groups of crested macaques living in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia over a period of 14 months.

METHODS

Study Site and Animals

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

Behavioural Data Collection

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

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

Dominance Rank

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

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

Body Weight

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

Vocal Recording & Acoustic Analysis

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

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

All calls were first inspected visually using SASLab Pro 4.39 (Avisoft Bioacoustics, Berlin, Germany) to make sure that background noises (e.g. bird song and other individuals calling) were not present in the recordings. The spectrogram settings that were applied for the extraction were: FFT length = 1024 points, window = Hamming, frame size = 100%, overlap = 96.87%. The resulting frequency resolution was 43 Hz at a time increment of 0.73 ms. After down sampling the recordings to 22.05 kHz, frequency resolution was 22 Hz at a time increment of 1.45 ms. All parameters were taken from down-sampled recordings, except frequency range for which the original sampling rate was kept. For one parameter (dominant frequency band), we applied a band pass filter to limit the frequency range of the signal, in order to measure the band between 0.7 and 1.5 kHz (f_{high} = 0.3 kHz, f_{low} = 2 kHz, see Figure 1). All spectrograms were saved as ASCII files for further processing. We then measured seven acoustic parameters: three temporal and four frequency parameters, which were suited to describe structural variations in loud calls (for detailed description see Fig. 1 and Table 2).

Statistical Analysis

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

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

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

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

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

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

RESULTS

Throughout the study, only males gave loud calls and all adult males of both study groups called regularly. **Loud calls were uttered to varying extents in the different contexts (aggression: 45.3%; feeding: 25.6%; resting: 10.2%; moving: 6.6%; social positive: 5.0%; mating: 3.9%; others, e.g. environmental stimuli: 3.3%; *N* = 1769 calls from 23 males). They** were short (mean ± **SE** = 0.418 ± 0.094 s, *N* = 194), pulsed vocalisations made up of two to nine distinct elements (Figure 1). From our observations it seemed that single elements were produced during exhalation. The main acoustic energy of single elements were distributed in two different frequency ranges, consisting of one small low frequency band (DFB) between 0.7 and 1.2 kHz and higher frequency band with a broader distribution of frequency energy between 2 and 8 kHz (**DFA3,** Fig. 1).

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

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

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

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

DISCUSSION

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

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

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

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

The observation that loud calls in crested macaques are only uttered by males while females of this species lack such a formal signal supports the hypothesis that in so called tolerant primate species (i.e. grade 4 species: Thierry 2000), status indicators should prevent contest and thus only occur if power is asymmetrically distributed over group members (Preuschoft & van Schaik 2000; Thierry 2004). **Female crested macaques are thought to experience only weak competition over resources and thus power asymmetries between females are small.** A status indicator preventing contest seems therefore unnecessary for them (Preuschoft & van Schaik 2000). Males, on the other hand, compete for fertile females – a resource that cannot be shared – with high-ranking males monopolising access to females (Rohr 2008), meaning that power is asymmetrically distributed among males (see also Reed et al. 1997). Hence, a divergence exists in the degree of intra-sexual competition between the sexes, which may explain the **occurrence** of a male specific signal of dominance, not only in crested macaques, but possibly also in other species with loud calls. In despotic species, in contrast, both sexes seem to face similar pressures of competition (though from different sources), which is thought to be the reason for the occurrence of status indicators in both sexes (Preuschoft & van Schaik 2000). Given the presence of a status indicator, male specific indicators should not be necessary and therefore not occur in despotic species. This line of argument may partly explain why loud calls occur only in some primate species and why they do not occur, for example, in pig-tailed macaques (*M. nemestrina*), the only macaque species of the silenus-group that is classified as despotic and the only one without male loud calls. In order to better understand the evolution of primate status indicators, it will be useful to investigate whether male signals of dominance occur only in those species in which male-male competition for females strongly outweighs female-female competition for resources.

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

Acknowledgments

We thank M. Heistermann, K. Hodges, C. Dubuc, C. Girard-Buttoz, J. Duboscq, T. Pizzari and three anonymous reviewers for critical discussions on the manuscript. We also wish to acknowledge all team members of the Macaca Nigra Project at Tangkoko Nature Reserve for supporting data collection. Furthermore, C.N. and A.E. want to thank Dr. Joko Pamungkas from the Primate Research Centre and Dr. Muhammad Agil from the Faculty of Veterinary Medicine, Bogor Agricultural University (IPB), for supporting their stay in Indonesia. This research was funded by the German Research Council, the Federal Ministry for Economic Cooperation and Development (EN719/1-1), the German Academic Exchange Service (DAAD), the Leakey Foundation and the German Primate Centre (DPZ). We gratefully acknowledge the permission of the Indonesian Institute of Sciences (LIPI), the Directorate General of Forest Protection and Nature Conservation (PHKA) and the Department for the Conservation of Natural Resources (BKSDA) in Manado, particularly Pak Domingus and Pak Yunus, to conduct research in the Tangkoko-Batuangus Nature Reserve.

References

Baker, S., Mulligan, B. E., Kohlhaas, A. & Pramono, A. H. 1991. "Loud calls" of *Macaca nigrescens* in Dumoga-Bone National Park, North Sulawesi [Abstract]. *American Journal of Primatology*, 24, 87-88.

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289-300.

Bradley, B. J. & Mundy, N. I. 2008. The primate palette: the evolution of primate coloration. *Evolutionary Anthropology*, 17, 97-111. doi:10.1002/evan.20164.

Chaffin, C. L., Friedlen, K. & de Waal, F. B. M. 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. *American Journal of Primatology*, 35, 103-116. doi:10.1002/ajp.1350350203.

Collins, N. M., Sayer, J. A. & Whitmore, T. C. 1991. *The conservation atlas of tropical forests: Asia and the Pacific*. New York: Simon & Schuster.

da Cunha, R. G. T. & Byrne, R. W. 2006. Roars of black howler monkeys (*Alouatta caraya*): evidence for a function in inter-group spacing. *Behaviour*, 143, 1169-1199. doi:10.1163/156853906778691568.

Darwin, C. 1876. Sexual selection in relation to monkeys. *Nature*, 15, 18-19. doi:10.1038/015018a0.

de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, 50, 1375-1389. doi:10.1016/0003-3472(95)80053-0.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, 55, 827-843. doi:10.1006/anbe.1997.0708.

de Waal, F. B. M. & Luttrell, L. M. 1985. The formal hierarchy of rhesus macaques - an investigation of the bared-teeth display. *American Journal of Primatology*, 9, 73-85. doi:10.1002/ajp.1350090202.

Delgado, R. A. 2006. Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology*, 27, 5-25. doi:10.1007/s10764-005-9001-4.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: *The macaques: studies in ecology, behavior, and evolution* (Ed. by D. G. Lindburg), pp. 10–30. Amsterdam: Van Nostrand Rheinhold.

Dingemanse, N. J. & de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, 15, 1023-1030. doi:10.1093/beheco/arh115.

Eberhardt, L. S. 1994. Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *The Auk*, 111, 124-130.

Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2002. Acoustic features of male baboon loud calls: influences of context, age, and individuality. *The Journal of the Acoustical Society of America*, 111, 1465-1474. doi:10.1121/1.1433807.

Fischer, J., Kitchen, D. M., Seyfarth, R. M. & Cheney, D. L. 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, 56, 140-148. doi:10.1007/s00265-003-0739-4.

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *The Journal of the Acoustical Society of America*, 102, 1213-1222. doi:10.1121/1.421048

Gautier, J. P. & Gautier, A. 1977. Communication in old world monkeys. In: *How animals communicate* (Ed. by T. A. Sebeok), pp. 890-964. Bloomington: Indiana University Press.

Gerhardt, H. C., Tanner, S. D., Corrigan, C. M. & Walton, H. C. 2000. Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral Ecology,* 11, 663-669. doi:10.1093/beheco/11.6.663.

Hammerschmidt, K. & Jürgens, U. 2007. Acoustical correlates of affective prosody. *Journal of Voice*, 21, 531–540. doi:10.1016/j.jvoice.2006.03.002.

Kinnaird, M. F. & O'Brien, T. G. 1999. A contextual analysis of the loud call of the Sulawesi crested black macaque, *Macaca nigra*. *Tropical Biodiversity,* 6, 37-42.

Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L. 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, 53, 374-384. doi:10.1007/s00265-003-0588-1.

Martin, P. & Bateson, P. 1993. *Measuring behaviour - an introductory guide*, 2nd edn. Cambridge: Cambridge University Press.

McComb, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, 41, 79-88. doi:10.1016/S0003-3472(05)80504-4.

Missakian, E. A. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates*, 13, 169-180. doi:10.1007/BF01840878.

Mitani, J. C. 1988. Male gibbon singing behavior: natural history, song variations and function. *Ethology*, 79, 177–194.

Mitani, J. C. & Stuht, J. 1998. The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates*, 39, 171-182. doi:10.1007/BF02557729.

Morton, E. S. 1977. On the occurence and significance of motivation-structural rules in some birds and mammal sounds. *The American Naturalist*, 111, 855-869. doi:10.1086/283219.

Mougeot, F., Irvine, J. R., Seivwright, L., Redpath, S. M. & Piertney, S. B. 2004. Testosterone, immunocompetence, and honest sexual signaling in male red grouse. *Behavioral Ecology*, 15, 930-937. doi:10.1093/beheco/arh087

Muroyama, Y. & Thierry, B. 1998. Species differences of male loud calls and their perception in Sulawesi macaques. *Primates*, 39, 115-126. doi: 10.1007/BF02557724.

Nunn, C. L. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, 58, 229-246. doi:10.1006/anbe.1999.1159

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351. doi:10.1023/A:1026330332061.

Okamoto, K. 2001. Loud calls in wild moor macaques (*Macaca maurus*): analysis on the movement of the emitter and group members before and after the call. *Tropical Biodiversity*, 7, 165-176.

Pfefferle, D. & Fischer, J. 2006. Sounds and size: identification of acoustic variables that reflect body size in hamdryas baboons, *Papio hamadryas*. *Animal Behaviour*, 72, 43-51. doi:10.1016/j.anbehav.2005.08.021

Preuschoft, S. 1995. "Laughter" and "smiling" in macaques: an evolutionary perspective, Faculteit Biologie, University Utrecht.

Preuschoft, S. & van Schaik, C. P. 2000. Dominance and communication - conflict management in various social settings. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 77-105. Berkely: University of California Press.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Raemaekers, J. J., Raemaekers, P. M. & Haimoff, E. H. 1984. Loud calls of the gibbon (*Hylobates lar*): repertoire, organization and context. *Behaviour*, 146-189. doi:10.1163/156853984X00263.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T. & Clutton-Brock, T. H. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B: Biological Sciences*, 272, 941-947. doi:10.1098/rspb.2004.2954.

Reed, C., O'Brien, T. G. & Kinnaird, M. F. 1997. Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 247-260. doi:10.1023/A:1026376720249.

Reichard, U. H. & Neumann, C. 2007. Long-distance solo calls of white-handed gibbon males (*Hylobates lar*) [Abstract]. *American Journal of Physical Anthropology*, 132, 196-197.

Riley, E. P. 2005. The loud call of the Sulawesi Tonkean macaque, *Macaca tonkeana*. *Tropical Biodiversity*, 8, 199-209.

Rohr, B. 2008. Female sexual behaviour during ovarian cycles in Sulawesi crested black macaques (*Macaca nigra*). Diploma Thesis, Freie Universität Berlin.

Rosenbaum, B., O'Brien, T. G., Kinnaird, M. F. & Supriatna, J. 1998. Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: effects of habitat disturbance and hunting. *American Journal of Primatology*, 44, 89-106. doi:10.1002/(SICI)1098-2345(1998)44:2<89::AID-AJP1>3.0.CO;2-S.

Schrader, L. & Hammerschmidt, K. 1997. Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach. *Bioacoustics*, 7, 247-265.

Snowdon, C. T. 2004. Sexual selection and communication. In: *Sexual selection in primates: New and comparative perspectives* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 57-70. Cambridge: Cambridge University Press.

Steenbeek, R., Assink, P. R. & Wich, S. A. 1999. Tenure related changes in wild Thomas's langurs II: loud calls. *Behaviour*, 136, 627-650. doi:10.1163/156853999501496.

Taigen, T. & Wells, K. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 155, 163-170. doi:10.1007/BF00685209.

Thierry, B. 2000. Covariation of conflict management patterns across macaque species. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 106-128. Berkely: University of California Press.

Thierry, B. 2004. Social epigenesis. In: *Macaque societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 267-294. Cambridge: Cambridge University Press.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, 16, 224-238. doi:10.1002/evan.20147.

Thierry, B., Bynum, E. L., Baker, S. C., Kinnaird, M. F., Matsumura, S., Muroyama, Y., O'Brien, T. G., Petit, O. & Watanabe, K. 2000. The social repertoire of Sulawesi macaques. *Primate Research*, 16, 203-226.

Tosi, A. J., Morales, J. C. & Melnick, D. J. 2003. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution*, 57, 1419-1435. doi:10.1111/j.0014-3820.2003.tb00349.x.

Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal signals: signalling and signal design in animal communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277-300. Trondheim: Tapir Academic Press.

Wagner, W. E. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour*, 44, 449-462. doi:10.1016/0003-3472(92)90055-E

Waser, P. M. 1982. The evolution of male loud calls among mangabeys and baboons. In: *Primate Communication* (Ed. by C. T. Snowdon, C. H. Brown & M. R. Petersen), pp. 117-143. Cambridge: Cambridge University Press.

Wich, S. A. & Nunn, C. L. 2002. Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology*, 52, 474-484. doi:10.1007/s00265-002-0541-8.

Wich, S. A., van der Post, D. J., Heistermann, M., Möhle, U., van Hooff, J. A. R. A. M. & Sterck, E. H. M. 2003. Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. *International Journal of Primatology*, 24, 1251-1265. doi:10.1023/B:IJOP.0000005991.97232.2a.

Figures' legends:

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

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

Table 1. Group membership, observation time, number of loud call recordings and dominance 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
Total		2743.5	194	

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

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

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

	Rank		**Context**	
Acoustic Parameter	*F* values	*P*	*F* values	*P*
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

Table 4: Relationship between acoustic parameters and body weight.

	Correlation with weight (*N* = 9 males)	
Parameter	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

Loud calls in male crested macaques (*Macaca nigra*) – a signal of dominance in a tolerant species

Christof Neumann[a,b], Gholib Assahad[c,d], Kurt Hammerschmidt[e],
Dyah Perwitasari-Farajallah[c,f], Antje Engelhardt[a,c,]*

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

[a] Department of Reproductive Biology, German Primate Centre, Göttingen, Germany
[b] Department of Animal Physiology, Faculty for Life Sciences, Pharmacy and Psychology, University Leipzig, Germany
[c] Primate Research Centre, Bogor Agricultural University, Indonesia
[d] Faculty of Veterinary Medicine, Bogor Agricultural University, Indonesia
[e] Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany
[f] Department of Biology, Faculty of Mathematics & Natural Sciences, Bogor Agricultural University, Indonesia

* Correspondence: Antje Engelhardt, Department of Reproductive Biology, Deutsches Primatenzentrum GmbH, Kellnerweg 4, 37077 Göttingen, Germany (email: aengelhardt@dpz.eu)

Word count: 4264

Abstract:

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

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

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

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

For primates, in contrast, it has for a long time been assumed that loud calls have not evolved through pressures of sexual selection, but are primarily used to mediate inter-group spacing and intra-group cohesion (e.g. Riley 2005; da Cunha & Byrne 2006). Results of a recent meta-analysis over the entire primate order however reveal that loud calls originally served to defend resources and to attract mates (Wich & Nunn 2002), and thus presumably still function in intra- and/or intersexual communication in a reproductive context. Although direct evidence for this hypothesis is still missing, the few existing studies on the function of loud calls lead to the conclusion that at least in some species, they represent a sexually selected trait. In male chacma baboons (*Papio cynocephalus ursinus*) for example, loud calls (‘wahoos’) signal dominance (Kitchen et al. 2003; Fischer et al. 2004) and play a role in male agonistic interactions, e.g. during male-male chases, suggesting that wahoos serve a function in male-male competition. In white-handed gibbons (*Hylobates lar*) and Thomas langurs (*Presbytis thomasii*), loud calls signal a males pairing status (Raemaekers et al. 1984; Reichard & Neumann 2007) and the life-phase he is in (see Steenbeek et al. 1999; Wich et al. 2003 for definition), respectively, suggesting that here, loud calls serve to attract females (but see Mitani 1988) and in orangutans, male loud calls may serve both, male-male competition and mate attraction (Delgado 2006). Apart from these studies, little is known about the information content and potential function of these vocalisations and more studies are clearly needed in order to better understand the adaptive significance of this trait in primates.

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

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

The aim of our study therefore was to investigate the information content of loud calls in crested macaques in the light of two concepts: sexual selection theory and macaque social style theory. Since crested macaques utter loud calls in different contexts (Kinnaird & O'Brien 1999) and the acoustic structure of these calls (and thus their information content and function) may vary with context (like in chacma baboons; Fischer et al. 2002), we first examined whether call structure varies in a context dependent manner. In a second step, we investigated whether loud calls meet two major criteria for sexually selected signals, i.e. whether the signal’s expression is sexually dimorphic and whether there is variation in the signal that can be assigned to individuals (Snowdon 2004). Furthermore, in order to investigate whether loud calls signal male dominance, we examined the relationship between the frequency of loud call utterance to selected acoustic call parameters and male dominance rank. As a potential measure of male fighting ability and quality, the relationship between male body weight, dominance rank and loud call characteristics were also examined. The study was carried out on two wild groups of crested macaques living in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia over a period of 14 months.

METHODS

Study Site and Animals

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

Behavioural Data Collection

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

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

Dominance Rank

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

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

Body Weight

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

Vocal Recording & Acoustic Analysis

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

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

All calls were first inspected visually using SASLab Pro 4.39 (Avisoft Bioacoustics, Berlin, Germany) to make sure that background noises (e.g. bird song and other individuals calling) were not present in the recordings. The spectrogram settings that were applied for the extraction were: FFT length = 1024 points, window = Hamming, frame size = 100%, overlap = 96.87%. The resulting frequency resolution was 43 Hz at a time increment of 0.73 ms. After down sampling the recordings to 22.05 kHz, frequency resolution was 22 Hz at a time increment of 1.45 ms. All parameters were taken from down-sampled recordings, except frequency range for which the original sampling rate was kept. For one parameter (dominant frequency band), we applied a band pass filter to limit the frequency range of the signal, in order to measure the band between 0.7 and 1.5 kHz (f_{high} = 0.3 kHz, f_{low} = 2 kHz, see Figure 1). All spectrograms were saved as ASCII files for further processing. We then measured seven acoustic parameters: three temporal and four frequency parameters, which were suited to describe structural variations in loud calls (for detailed description see Fig. 1 and Table 2).

Statistical Analysis

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

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

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

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

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

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

RESULTS

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

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

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

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

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

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

DISCUSSION

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

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

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

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

The observation that loud calls in crested macaques are only uttered by males while females of this species lack such a formal signal supports the hypothesis that in so called tolerant primate species (i.e. grade 4 species: Thierry 2000), status indicators should prevent contest and thus only occur if power is asymmetrically distributed over group members (Preuschoft & van Schaik 2000; Thierry 2004). Female crested macaques are thought to experience only weak competition over resources and thus power asymmetries between females are small. A status indicator preventing contest seems therefore unnecessary for them (Preuschoft & van Schaik 2000). Males, on the other hand, compete for fertile females – a resource that cannot be shared – with high-ranking males monopolising access to females (Rohr 2008), meaning that power is asymmetrically distributed among males (see also Reed et al. 1997). Hence, a divergence exists in the degree of intra-sexual competition between the sexes, which may explain the occurrence of a male specific signal of dominance, not only in crested macaques, but possibly also in other species with loud calls. In despotic species, in contrast, both sexes seem to face similar pressures of competition (though from different sources), which is thought to be the reason for the occurrence of status indicators in both sexes (Preuschoft & van Schaik 2000). Given the presence of a status indicator, male specific indicators should not be necessary and therefore not occur in despotic species. This line of argument may partly explain why loud calls occur only in some primate species and why they do not occur, for example, in pig-tailed macaques (*M. nemestrina*), the only macaque species of the silenus-group that is classified as despotic and the only one without male loud calls. In order to better understand the evolution of primate status indicators, it will be useful to investigate whether male signals of dominance occur only in those species in which male-male competition for females strongly outweighs female-female competition for resources.

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

Acknowledgments

We thank M. Heistermann, K. Hodges, C. Dubuc, C. Girard-Buttoz, J. Duboscq, T. Pizzari and three anonymous reviewers for critical discussions on the manuscript. We also wish to acknowledge all team members of the Macaca Nigra Project at Tangkoko Nature Reserve for supporting data collection. Furthermore, C.N. and A.E. want to thank Dr. Joko Pamungkas from the Primate Research Centre and Dr. Muhammad Agil from the Faculty of Veterinary Medicine, Bogor Agricultural University (IPB), for supporting their stay in Indonesia. This research was funded by the German Research Council, the Federal Ministry for Economic Cooperation and Development (EN719/1-1), the German Academic Exchange Service (DAAD), the Leakey Foundation and the German Primate Centre (DPZ). We gratefully acknowledge the permission of the Indonesian Institute of Sciences (LIPI), the Directorate General of Forest Protection and Nature Conservation (PHKA) and the Department for the Conservation of Natural Resources (BKSDA) in Manado, particularly Pak Domingus and Pak Yunus, to conduct research in the Tangkoko-Batuangus Nature Reserve.

References

Baker, S., Mulligan, B. E., Kohlhaas, A. & Pramono, A. H. 1991. "Loud calls" of *Macaca nigrescens* in Dumoga-Bone National Park, North Sulawesi [Abstract]. *American Journal of Primatology*, 24, 87-88.

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289-300.

Bradley, B. J. & Mundy, N. I. 2008. The primate palette: the evolution of primate coloration. *Evolutionary Anthropology*, 17, 97-111. doi:10.1002/evan.20164.

Chaffin, C. L., Friedlen, K. & de Waal, F. B. M. 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. *American Journal of Primatology*, 35, 103-116. doi:10.1002/ajp.1350350203.

Collins, N. M., Sayer, J. A. & Whitmore, T. C. 1991. *The conservation atlas of tropical forests: Asia and the Pacific*. New York: Simon & Schuster.

da Cunha, R. G. T. & Byrne, R. W. 2006. Roars of black howler monkeys (*Alouatta caraya*): evidence for a function in inter-group spacing. *Behaviour*, 143, 1169-1199. doi:10.1163/156853906778691568.

Darwin, C. 1876. Sexual selection in relation to monkeys. *Nature*, 15, 18-19. doi:10.1038/015018a0.

de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, 50, 1375-1389. doi:10.1016/0003-3472(95)80053-0.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, 55, 827-843. doi:10.1006/anbe.1997.0708.

de Waal, F. B. M. & Luttrell, L. M. 1985. The formal hierarchy of rhesus macaques - an investigation of the bared-teeth display. *American Journal of Primatology*, 9, 73-85. doi:10.1002/ajp.1350090202.

Delgado, R. A. 2006. Sexual selection in the loud calls of male primates: signal content and function. *International Journal of Primatology*, 27, 5-25. doi:10.1007/s10764-005-9001-4.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: *The macaques: studies in ecology, behavior, and evolution* (Ed. by D. G. Lindburg), pp. 10–30. Amsterdam: Van Nostrand Rheinhold.

Dingemanse, N. J. & de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, 15, 1023-1030. doi:10.1093/beheco/arh115.

Eberhardt, L. S. 1994. Oxygen consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *The Auk*, 111, 124-130.

Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2002. Acoustic features of male baboon loud calls: influences of context, age, and individuality. *The Journal of the Acoustical Society of America*, 111, 1465-1474. doi:10.1121/1.1433807.

Fischer, J., Kitchen, D. M., Seyfarth, R. M. & Cheney, D. L. 2004. Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, 56, 140-148. doi:10.1007/s00265-003-0739-4.

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *The Journal of the Acoustical Society of America*, 102, 1213-1222. doi:10.1121/1.421048

Gautier, J. P. & Gautier, A. 1977. Communication in old world monkeys. In: *How animals communicate* (Ed. by T. A. Sebeok), pp. 890-964. Bloomington: Indiana University Press.

Gerhardt, H. C., Tanner, S. D., Corrigan, C. M. & Walton, H. C. 2000. Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral Ecology*, 11, 663-669. doi:10.1093/beheco/11.6.663.

Hammerschmidt, K. & Jürgens, U. 2007. Acoustical correlates of affective prosody. *Journal of Voice*, 21, 531–540. doi:10.1016/j.jvoice.2006.03.002.

Kinnaird, M. F. & O'Brien, T. G. 1999. A contextual analysis of the loud call of the Sulawesi crested black macaque, *Macaca nigra*. *Tropical Biodiversity*, 6, 37-42.

Kitchen, D. M., Seyfarth, R. M., Fischer, J. & Cheney, D. L. 2003. Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology*, 53, 374-384. doi:10.1007/s00265-003-0588-1.

Martin, P. & Bateson, P. 1993. *Measuring behaviour - an introductory guide*, 2nd edn. Cambridge: Cambridge University Press.

McComb, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, 41, 79-88. doi:10.1016/S0003-3472(05)80504-4.

Missakian, E. A. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates*, 13, 169-180. doi:10.1007/BF01840878.

Mitani, J. C. 1988. Male gibbon singing behavior: natural history, song variations and function. *Ethology,* 79, 177–194.

Mitani, J. C. & Stuht, J. 1998. The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates*, 39, 171-182. doi:10.1007/BF02557729.

Morton, E. S. 1977. On the occurence and significance of motivation-structural rules in some birds and mammal sounds. *The American Naturalist*, 111, 855-869. doi:10.1086/283219.

Mougeot, F., Irvine, J. R., Seivwright, L., Redpath, S. M. & Piertney, S. B. 2004. Testosterone, immunocompetence, and honest sexual signaling in male red grouse. *Behavioral Ecology*, 15, 930-937. doi:10.1093/beheco/arh087

Muroyama, Y. & Thierry, B. 1998. Species differences of male loud calls and their perception in Sulawesi macaques. *Primates,* 39, 115-126. doi: 10.1007/BF02557724.

Nunn, C. L. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour,* 58, 229-246. doi:10.1006/anbe.1999.1159

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351. doi:10.1023/A:1026330332061.

Okamoto, K. 2001. Loud calls in wild moor macaques (*Macaca maurus*): analysis on the movement of the emitter and group members before and after the call. *Tropical Biodiversity*, 7, 165-176.

Pfefferle, D. & Fischer, J. 2006. Sounds and size: identification of acoustic variables that reflect body size in hamdryas baboons, *Papio hamadryas*. *Animal Behaviour*, 72, 43-51. doi:10.1016/j.anbehav.2005.08.021

Preuschoft, S. 1995. "Laughter" and "smiling" in macaques: an evolutionary perspective, Faculteit Biologie, University Utrecht.

Preuschoft, S. & van Schaik, C. P. 2000. Dominance and communication - conflict management in various social settings. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 77-105. Berkely: University of California Press.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Raemaekers, J. J., Raemaekers, P. M. & Haimoff, E. H. 1984. Loud calls of the gibbon (*Hylobates lar*): repertoire, organization and context. *Behaviour*, 146-189. doi:10.1163/156853984X00263.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T. & Clutton-Brock, T. H. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B: Biological Sciences*, 272, 941-947. doi:10.1098/rspb.2004.2954.

Reed, C., O'Brien, T. G. & Kinnaird, M. F. 1997. Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 247-260. doi:10.1023/A:1026376720249.

Reichard, U. H. & Neumann, C. 2007. Long-distance solo calls of white-handed gibbon males (*Hylobates lar*) [Abstract]. *American Journal of Physical Anthropology*, 132, 196-197.

Riley, E. P. 2005. The loud call of the Sulawesi Tonkean macaque, *Macaca tonkeana*. *Tropical Biodiversity*, 8, 199-209.

Rohr, B. 2008. Female sexual behaviour during ovarian cycles in Sulawesi crested black macaques (*Macaca nigra*). Diploma Thesis, Freie Universität Berlin.

Rosenbaum, B., O'Brien, T. G., Kinnaird, M. F. & Supriatna, J. 1998. Population densities of Sulawesi crested black macaques (*Macaca nigra*) on Bacan and Sulawesi, Indonesia: effects of habitat disturbance and hunting. *American Journal of Primatology*, 44, 89-106. doi:10.1002/(SICI)1098-2345(1998)44:2<89::AID-AJP1>3.0.CO;2-S.

Schrader, L. & Hammerschmidt, K. 1997. Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach. *Bioacoustics*, 7, 247-265.

Snowdon, C. T. 2004. Sexual selection and communication. In: *Sexual selection in primates: New and comparative perspectives* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 57-70. Cambridge: Cambridge University Press.

Steenbeek, R., Assink, P. R. & Wich, S. A. 1999. Tenure related changes in wild Thomas's langurs II: loud calls. *Behaviour*, 136, 627-650. doi:10.1163/156853999501496.

Taigen, T. & Wells, K. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 155, 163-170. doi:10.1007/BF00685209.

Thierry, B. 2000. Covariation of conflict management patterns across macaque species. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 106-128. Berkely: University of California Press.

Thierry, B. 2004. Social epigenesis. In: *Macaque societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 267-294. Cambridge: Cambridge University Press.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, 16, 224-238. doi:10.1002/evan.20147.

Thierry, B., Bynum, E. L., Baker, S. C., Kinnaird, M. F., Matsumura, S., Muroyama, Y., O'Brien, T. G., Petit, O. & Watanabe, K. 2000. The social repertoire of Sulawesi macaques. *Primate Research*, 16, 203-226.

Tosi, A. J., Morales, J. C. & Melnick, D. J. 2003. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution*, 57, 1419-1435. doi:10.1111/j.0014-3820.2003.tb00349.x.

Vehrencamp, S. L. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal signals: signalling and signal design in animal communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277-300. Trondheim: Tapir Academic Press.

Wagner, W. E. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Animal Behaviour*, 44, 449-462. doi:10.1016/0003-3472(92)90055-E

Waser, P. M. 1982. The evolution of male loud calls among mangabeys and baboons. In: *Primate Communication* (Ed. by C. T. Snowdon, C. H. Brown & M. R. Petersen), pp. 117-143. Cambridge: Cambridge University Press.

Wich, S. A. & Nunn, C. L. 2002. Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. *Behavioral Ecology and Sociobiology*, 52, 474-484. doi:10.1007/s00265-002-0541-8.

Wich, S. A., van der Post, D. J., Heistermann, M., Möhle, U., van Hooff, J. A. R. A. M. & Sterck, E. H. M. 2003. Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. *International Journal of Primatology*, 24, 1251-1265. doi:10.1023/B:IJOP.0000005991.97232.2a.

Figures' legends:

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

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

Table 1. Group membership, observation time, number of loud call recordings and dominance 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
Total		2743.5	194	

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

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

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

	Rank		**Context**	
Acoustic Parameter	*F* values	*P*	*F* values	*P*
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

Table 4: Relationship between acoustic parameters and body weight.

	Correlation with weight (N = 9 males)	
Parameter	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

Figure 1

Click here to download high resolution image

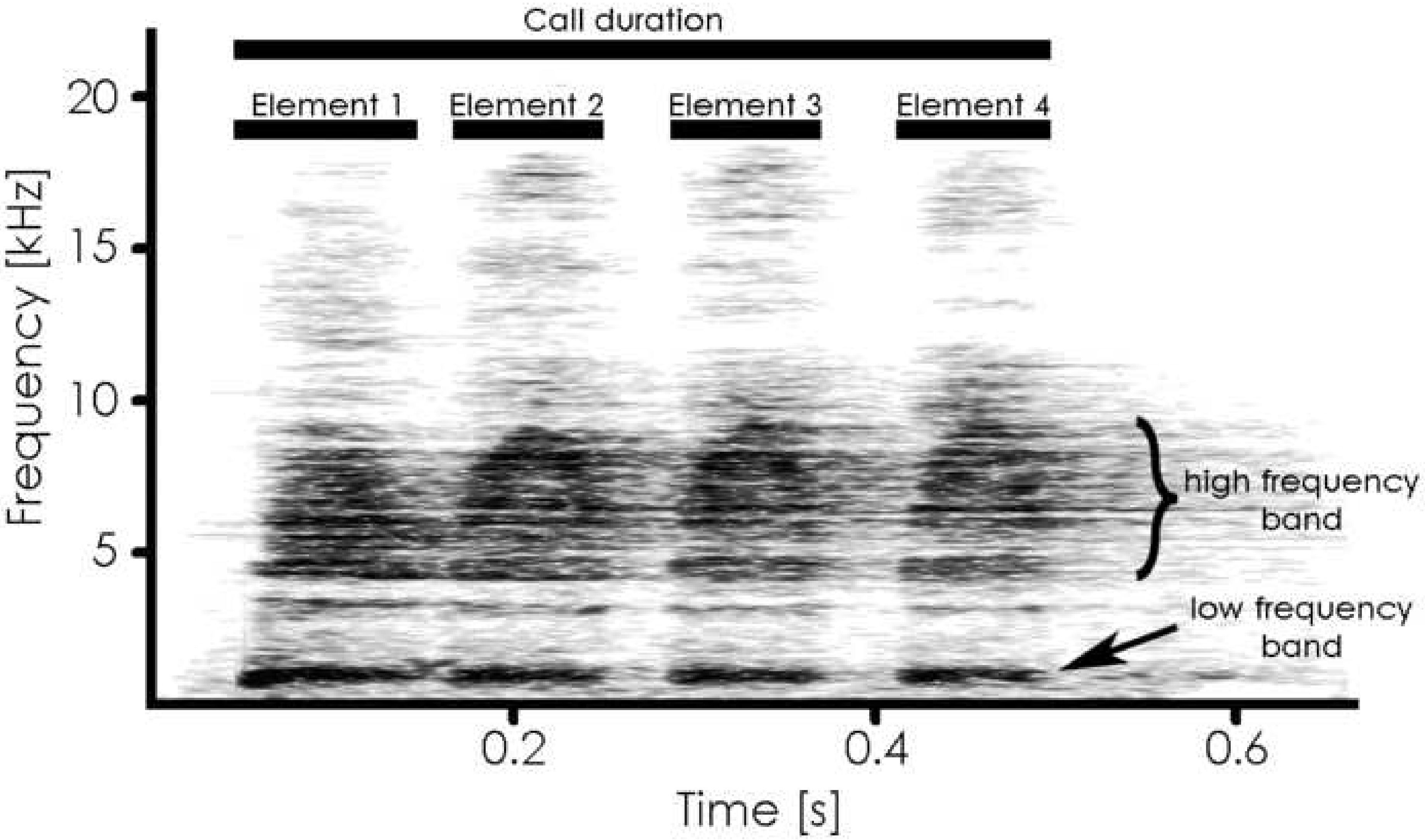
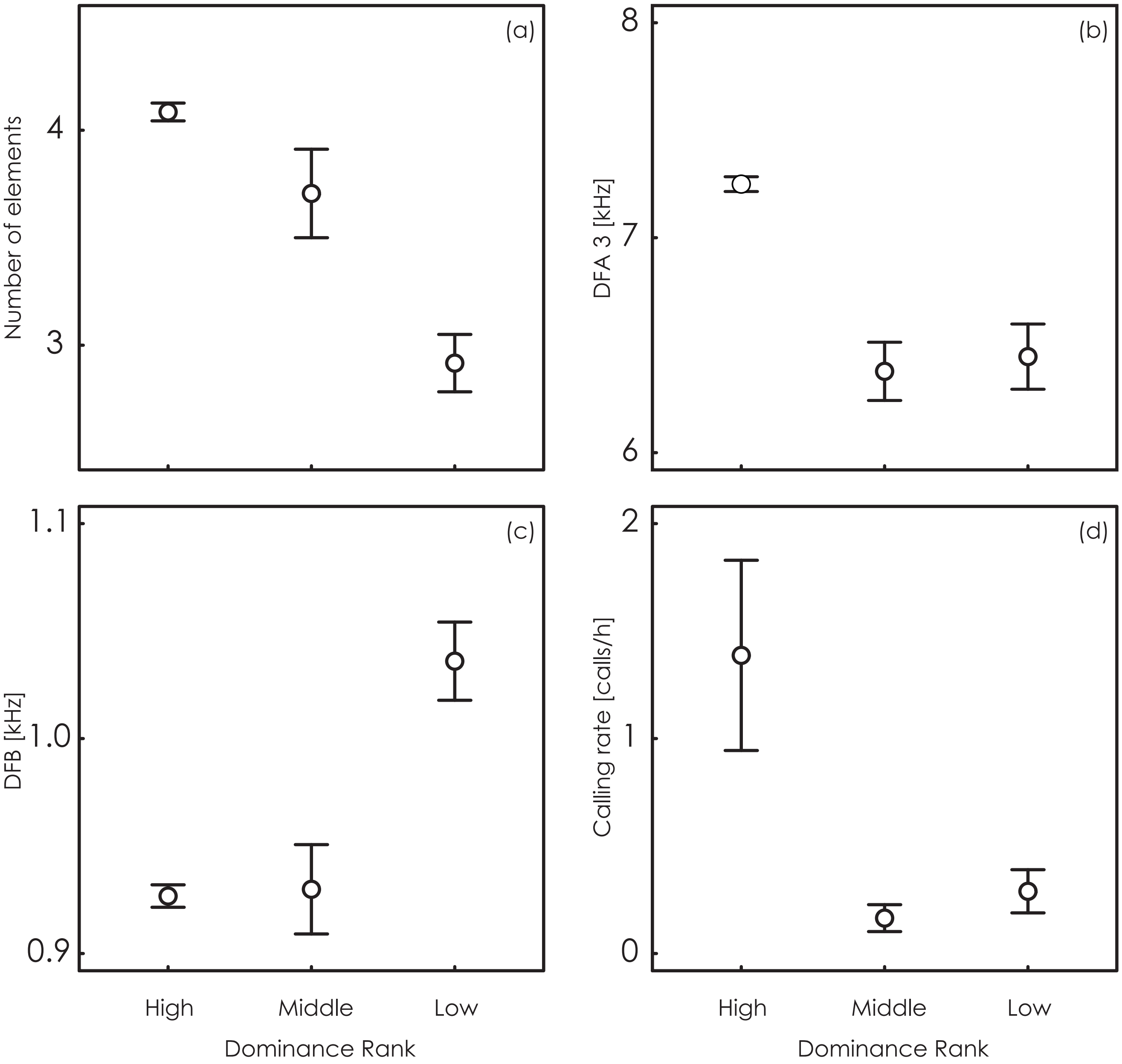


Figure 2


(a)
Number of elements
4
3
(b)
DFA 3 [kHz]
8
7
6
(c)
DFB [kHz]
1.1
1.0
0.9
(d)
Calling rate [calls/h]
2
1
0
High
Middle
Low
Dominance Rank
High
Middle
Low
Dominance Rank

Publicity Photograph (Optional)

Click here to download high resolution image

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.