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

Christof Neumann[a, b], Gholib Assahad[c, d, 1], Kurt Hammerschmidt[e], Dyah Perwitasari-Farajallah[c, f, 1] and Antje Engelhardt[a, c,]

[a] Department of Reproductive Biology, German Primate Centre, 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, Germany
[f] Department of Biology, Faculty of Mathematics & Natural Sciences, Bogor Agricultural University, Indonesia

Received 26 September 2008;
revised 19 January 2009;
accepted 16 October 2009.
MS. number: 08-00623R.

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 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 by 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, however, was not influenced by context. Our findings consolidate the assumption that, in crested macaques, loud calls serve as a signal of dominance, most probably used to prevent contests between males for mates. We herewith provide the first direct evidence for a signal of dominance in a tolerant primate species and discuss why this signal occurs in only one sex.

Keywords: crested macaque; dominance signal; loud call; *Macaca nigra*; sexual selection; sexual signal; social style

Article Outline

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

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 (intrasexual selection) by signalling competitive abilities to contestants (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 (intersexual selection) by signalling individual quality to them (e.g. red deer: McComb 1991; grey treefrog, *Hyla versicolor*: Gerhardt et al. 2000; red grouse, *Lagopus lagopus scoticus*: Mougeot et al. 2004).

For primates, in contrast, it has long been assumed that loud calls have not evolved through pressures of sexual selection, but are primarily used to mediate intergroup spacing and intragroup cohesion (e.g. [Riley, 2005] and [da Cunha and 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] and [Fischer et al., 2004]) and play a role in male agonistic interactions, for example 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 male's pairing status ([Raemaekers et al., 1984] and [Reichard and Neumann, 2007]) and the life phase he is in (see [Steenbeek et al., 1999] and [Wich et al., 2003] for definition), respectively, suggesting that, here, loud calls serve to attract females (but see Mitani 1988) and in orang-utans, *Pongo pygmaeus*, 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 vocalizations and more studies are clearly needed to improve our understanding of the adaptive significance of this trait in primates.

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

Crested macaques 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 multimale multifemale, 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*) utter loud calls ([Delson, 1980] and [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 vocalize, whereas in the other macaques calling is mainly limited to alpha males ([Baker et al., 1991], [Okamoto, 2001] and [Riley, 2005]). So far, macaque loud calls have been interpreted to serve a function for intergroup 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 has examined the possibility that loud calls in 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) and (Thierry, 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 and van Schaik, 2000] and [Thierry, 2004]). Although there is ample evidence for signals of submission in despotic macaques (grades 1–2) and for signals of dominance in slightly tolerant macaques (grade 3; [de Waal and Luttrell, 1985], [Chaffin et al., 1995] and [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 wild 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 (as 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, that is, 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, 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 relationships between male body weight, dominance rank and loud call characteristics were also examined.

Methods

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

Study Site and Animals

We studied two groups of free-ranging, wild crested macaques from July 2006 to August 2007 in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia (1°33′ N, 125°10′ E). The reserve comprises an area of 8867 ha lowland rainforest, and ranges from sea level to 1350 m ([Collins et al., 1991] and [Rosenbaum et al., 1998]). Two multimale 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 10 years ([O'Brien and Kinnaird, 1997], [Reed et al., 1997] and [Kinnaird and 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 h of focal observation time (mean focal time per male: 119.3 h; range 10.8–170.9 h; Table 1). Each male was followed once a week, alternating from the male's descent from the sleeping tree to noon and from noon to the time the focal male entered the sleeping tree. We used instantaneous sampling (Martin & Bateson 1993) with an interval of 1 min for the focal animal's activity, noting the occurrence of loud calls, social interactions (sociopositive and agonistic behaviour, mating) and displacement interactions between males as continuous events. Agonistic and displacement interactions between males were furthermore recorded ad libitum.

Table 1.

Group membership, observation time, number of loud call recordings and dominance rank class of the study males

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

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

Male	Group	Observation time (h)	Recorded loud calls	Rank class
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[†]	153.1	34	Middle, high
Total		2743.5	194	

[*] Body weights were obtained for these males.
[†] ZJ migrated from R1 to R2 during the study and replaced SJ as alpha male in R2.

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 owing 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. We took into account only conflicts that did not include counteraggression by the 'victim/loser', that is, only unidirectional interactions.

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

We then tested whether it was justified to rank males linearly by means of de Vries's (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 that expected by chance is $P = 0.028$ (maximum $P = 0.069$). Even though three 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, that is, 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).

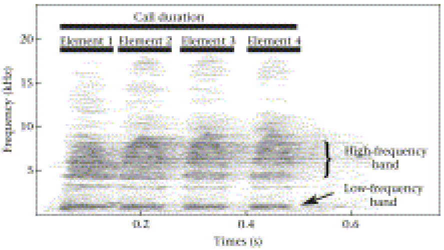
Body Weight

We weighed adult males by positioning a digital scale (modified Combics scale, Sartorius, Göttingen, Germany, weight step = 0.02 kg) at a fixed location and luring single males 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. Measurements were only taken into account if a male was weighed at least twice during one weighing session.

Vocal Recording and Acoustic Analysis

Loud calls were recorded ad libitum and the context in which the call occurred was noted. Recordings were made with a digital portable solid state recorder (PMD660, Marantz, Itasca, IL, U.S.A.) and a directional microphone (K6-ME66, Sennheiser, Wedemark, Germany) equipped with a windshield (265E, Rycote, Gloucestershire, U.K.) at a sampling rate of 44.1 kHz. We recorded a total of 194 loud calls of sufficient quality for analysis from six contexts: (1) aggression = calls given during or immediately after an aggressive interaction, $N = 40$; (2) resting = calls given outside any obvious context, that is, during resting periods, $N = 57$; (3) feeding = calls given during feeding or foraging activity, $N = 8$; (4) moving = calls given during group movement, $N = 13$; (5) social positive = calls that occurred in or followed affiliative interactions, such as grooming, male–male mounting, genital grasp, $N = 12$; (6) mating = calls uttered 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. birdsong 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 (high-pass filter = 0.3 kHz, low-pass filter = 2 kHz, i.e. frequencies below 0.3 kHz and above 2 kHz were filtered out; see Fig. 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 suitable for describing structural variations in loud calls (for detailed description see Fig. 1 and Table 2).



Full-size image (32K)

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.

Table 2.

Description of acoustic parameters

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/s)
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 1 SD) as calculated from the adjacent frequency bins. In tonal calls the (lowest) DFB corresponds to the fundamental frequency

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

Acoustic parameter	**Description**
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 characterizes 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

Full-size table

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 & Hammerschmidt (1997).

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 factors, 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 rank correlation. For this, we calculated mean parameter values of all calls of a given male while he was in one rank class and used these means to correlate them with body weight.

For each male, the mean frequency of call utterance (loud calls/h) 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 (SPSS Inc., Chicago, IL, U.S.A.) 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 & 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 vocalizations made up of two to nine distinct elements (Fig. 1). From our observations it seemed that single elements were produced during exhalation. The main acoustic energy of single elements was distributed in two different frequency ranges, consisting of one small, low-frequency band (DFB) between 0.7 and 1.2 kHz and a 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, after Hochberg correction, related to context (Table 3). High-ranking males produced loud calls containing more elements than middle- and low-ranking males (Fig. 2a). In addition, call elements of high-ranking males showed a significantly higher frequency in their second broader frequency band than middle- and low-ranking males (Fig. 2b). However, high- and middle-ranking males did not differ in their low-frequency band, and only low-ranking males produced DFBs with a higher frequency (Fig. 2c).

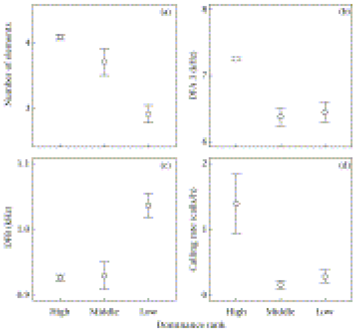
Table 3.

Rank- and context-related differences in acoustic structure of loud calls of male crested macaques

Acoustic parameter	**Rank**		**Context**	
	F	***P***	***F***	***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

Acoustic parameter	**Rank**		**Context**	
	F	***P***	***F***	***P***
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

Significant differences after Hochberg correction are marked by bold values.



Full-size image (27K)

Figure 2. Dominance-related differences in acoustic structure and calling rate of male loud calls (mean and SE). (a) Number of elements, (b) high-frequency band (measured as DFA3), (c) low-frequency band (DFB) and (d) calling rate (calls/h).

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 ($\chi_2^2 = 9.156$, $P = 0.010$), with high-ranking males calling more often than middle- and low-ranking males (Fig. 2d). In particular, alpha males called at high rates and gave on average 3.0 loud calls/h (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: $\chi_2^2 = 1.242$, $P = 0.537$).

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

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

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: (1) they were only uttered by males (and are thus sexually dimorphic) and (2) 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 loud calls uttered, 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 social contexts varied significantly (e.g. mating versus aggression). Apparently, in crested macaques, loud calls cannot 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] and [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 bear energetic costs (Fischer et al. 2004; see also [Taigen and Wells, 1985] and [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 reflected not only 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 nontonal 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, however, this hypothesis has received little support so far, first because dominance seems to be a multifactorial phenomenon in most animal taxa and is not usually affected only by body size (e.g. [Missakian, 1972] and [Dingemanse and de Goede, 2004]), and second because fundamental frequency is only weakly correlated with body size in most vertebrates including primates ([McComb, 1991] and [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 that 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 also does 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 not only encoded male dominance rank through low frequencies. Together with lower DFBs, high-ranking males also produced higher-pitched calls, that is, calls with higher DFA3. This finding again contradicts Morton's predictions, 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 at both extremes and how far spectral parameters of loud calls represent male quality other than mere competitive ability in crested macaques (e.g. major histocompatibility complex) need 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 contestants even when they occur within the context of aggression. Whereas in baboons loud calls thus seem to prevent contest escalation, crested macaques may use loud calls to avoid contests in the first place. This conclusion is also supported by the observation that loud calls are uttered not only during aggression, but also during other contexts. However, further investigation into the effect of loud calls on the frequency of male contests is needed to clarify further 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 contests and thus only occur if power is asymmetrically distributed over group members ([Preuschoft and van Schaik, 2000] and [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 contests therefore seems 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 monopolizing access to females (Rohr 2008); power is thus asymmetrically distributed among males (see also Reed et al. 1997). Hence, a divergence exists in the degree of intrasexual 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 (although 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 should 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 pigtailed macaques, *M. nemestrina*, a macaque species of the silenus group that is classified as despotic and one without male loud calls. To understand the evolution of primate status indicators better, it will be useful to investigate whether male specific 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 being, however, 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 vocalizations represent a sexually selected trait in this species, possibly serving to prevent contests 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 intrasexual selection and 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 examine criteria ascribed to sexual signals further (Snowdon 2004), investigating to what extent loud calls occur in the context of reproduction, how they affect male contests, whether they attract females and 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 referees for critical discussions on the manuscript. We also acknowledge all team members of the Macaca Nigra Project at Tangkoko Nature Reserve for supporting data collection. Furthermore, C.N. and A.E. 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 et al., 1991 S. Baker, B.E. Mulligan, A. Kohlhaas and A.H. Pramono, ‘Loud calls’ of *Macaca nigrescens* in Dumoga-Bone National Park, North Sulawesi, *American Journal of Primatology* **24** (1991), pp. 87–88 [Abstract].

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

Bradley and Mundy, 2008 B.J. Bradley and N.I. Mundy, The primate palette: the evolution of primate coloration, *Evolutionary Anthropology* **17** (2008), pp. 97–111 10.1002/evan.20164. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (11)

Chaffin et al., 1995 C.L. Chaffin, K. Friedlen and F.B.M. de Waal, Dominance style of Japanese macaques compared with rhesus and stumptail macaques, *American Journal of Primatology* **35** (1995), pp. 103–116 10.1002/ajp.1350350203. **Full Text** via CrossRef

Collins et al., 1991 N.M. Collins, J.A. Sayer and T.C. Whitmore, The Conservation Atlas of Tropical Forests: Asia and the Pacific, Simon & Schuster, New York (1991).

da Cunha and Byrne, 2006 R.G.T. da Cunha and R.W. Byrne, Roars of black howler monkeys (*Alouatta caraya*): evidence for a function in inter-group spacing, *Behaviour* **143** (2006), pp. 1169–1199 10.1163/156853906778691568. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (6)

Darwin, 1876 C. Darwin, Sexual selection in relation to monkeys, *Nature* **15** (1876), pp. 18–19 10.1038/015018a0. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (19)

Delgado, 2006 R.A. Delgado, Sexual selection in the loud calls of male primates: signal content and function, *International Journal of Primatology* **27** (2006), pp. 5–25 10.1007/s10764-005-9001-4. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (7)

Delson, 1980 E. Delson, Fossil macaques, phyletic relationships and a scenario of deployment. In: D.G. Lindburg, Editor, *The Macaques: Studies in Ecology, Behavior, and Evolution*, Van Nostrand Rheinhold, Amsterdam (1980), pp. 10–30.

Dingemanse and de Goede, 2004 N.J. Dingemanse and P. de Goede, The relation between dominance and exploratory behavior is context-dependent in wild great tits, *Behavioral Ecology* **15** (2004), pp. 1023–1030 10.1093/beheco/arh115. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (42)

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

Fischer et al., 2002 J. Fischer, K. Hammerschmidt, D.L. Cheney and R.M. Seyfarth, Acoustic features of male baboon loud calls: influences of context, age, and individuality, *Journal of the Acoustical Society of America* **111** (2002), pp. 1465–1474 10.1121/1.1433807. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (54)

Fischer et al., 2004 J. Fischer, D.M. Kitchen, R.M. Seyfarth and D.L. Cheney, Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion, *Behavioral Ecology and Sociobiology* **56** (2004), pp. 140–148 10.1007/s00265-003-0739-4. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (52)

Fitch, 1997 W.T. Fitch, Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques, *Journal of the Acoustical Society of America* **102** (1997), pp. 1213–1222 10.1121/1.421048. OJPS full text | **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (169)

Gautier and Gautier, 1977 J.P. Gautier and A. Gautier, Communication in old world monkeys. In: T.A. Sebeok, Editor, *How Animals Communicate*, Indiana University Press, Bloomington (1977), pp. 890–964.

Gerhardt et al., 2000 H.C. Gerhardt, S.D. Tanner, C.M. Corrigan and H.C. Walton, Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*), *Behavioral Ecology* **11** (2000), pp. 663–669 10.1093/beheco/11.6.663. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (47)

Hammerschmidt and Jürgens, 2007 K. Hammerschmidt and U. Jürgens, Acoustical correlates of affective prosody, *Journal of Voice* **21** (2007), pp. 531–540 10.1016/j.jvoice.2006.03.002. **Article** | PDF (257 K) | View Record in Scopus | Cited By in Scopus (7)

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

Kitchen et al., 2003 D.M. Kitchen, R.M. Seyfarth, J. Fischer and D.L. Cheney, Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*), *Behavioral Ecology and Sociobiology* **53** (2003), pp. 374–384 10.1007/s00265-003-0588-1. View Record in Scopus | Cited By in Scopus (55)

McComb, 1991 K. McComb, Female choice for high roaring rates in red deer, *Cervus elaphus*, *Animal Behaviour* **41** (1991), pp. 79–88 10.1016/S0003-3472(05)80504-4. Abstract | PDF (836 K) | View Record in Scopus | Cited By in Scopus (72)

Martin and Bateson, 1993 P. Martin and P. Bateson, Measuring Behaviour: an Introductory Guide (2nd edn), Cambridge University Press, Cambridge (1993).

Missakian, 1972 E.A. Missakian, Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago, *Primates* **13** (1972), pp. 169–180 10.1007/BF01840878. View Record in Scopus | Cited By in Scopus (25)

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

Mitani and Stuht, 1998 J.C. Mitani and J. Stuht, The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission, *Primates* **39** (1998), pp. 171–182 10.1007/BF02557729. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (19)

Morton, 1977 E.S. Morton, On the occurence and significance of motivation-structural rules in some birds and mammal sounds, *American Naturalist* **111** (1977), pp. 855–869 10.1086/283219. **Full Text** via CrossRef

Mougeot et al., 2004 F. Mougeot, J.R. Irvine, L. Seivwright, S.M. Redpath and S.B. Piertney, Testosterone, immunocompetence, and honest sexual signaling in male red grouse, *Behavioral Ecology* **15** (2004), pp. 930–937 10.1093/beheco/arh087. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (34)

Muroyama and Thierry, 1998 Y. Muroyama and B. Thierry, Species differences of male loud calls and their perception in Sulawesi macaques, *Primates* **39** (1998), pp. 115–126 10.1007/BF02557724. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (5)

Nunn, 1999 C.L. Nunn, The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis, *Animal Behaviour* **58** (1999), pp. 229–246 10.1006/anbe.1999.1159. Abstract | PDF (331 K) | View Record in Scopus | Cited By in Scopus (107)

O'Brien and Kinnaird, 1997 T.G. O'Brien and M.F. Kinnaird, Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*), *International Journal of Primatology* **18** (1997), pp. 321–351 10.1023/A:1026330332061. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (30)

Okamoto, 2001 K. Okamoto, 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** (2001), pp. 165–176.

Pfefferle and Fischer, 2006 D. Pfefferle and J. Fischer, Sounds and size: identification of acoustic variables that reflect body size in hamdryas baboons, *Papio hamadryas*, *Animal Behaviour* **72** (2006), pp. 43–51 10.1016/j.anbehav.2005.08.021. **Article** | PDF (431 K) | View Record in Scopus | Cited By in Scopus (29)

Preuschoft, 1995 **Preuschoft, S.** 1995. ‘Laughter’ and ‘smiling’ in macaques: an evolutionary perspective. Ph.D. thesis, Faculteit Biologie, University Utrecht.

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

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

Raemaekers et al., 1984 J.J. Raemaekers, P.M. Raemaekers and E.H. Haimoff, Loud calls of the gibbon (*Hylobates lar*): repertoire, organization and context, *Behaviour* (1984), pp. 146–189 10.1163/156853984X00263. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (26)

Reby et al., 2005 D. Reby, K. McComb, B. Cargnelutti, C. Darwin, W.T. Fitch and T.H. Clutton-Brock, Red deer stags use formants as assessment cues during intrasexual agonistic interactions, *Proceedings of the Royal Society B* **272** (2005), pp. 941–947 10.1098/rspb.2004.2954. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (44)

Reed et al., 1997 C. Reed, T.G. O'Brien and M.F. Kinnaird, Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*), *International Journal of Primatology* **18** (1997), pp. 247–260 10.1023/A:1026376720249. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (8)

http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6W9W-4XRJGTF-2&_user=6763742&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1372367829&_rerunOrigin=scholar.google&_acct=C000070526&_version=1&_urlVersion=0&_userid=6763742&md5=ad070a88c726def4f9b69e765d9173d7

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

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

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

Rosenbaum et al., 1998 B. Rosenbaum, T.G. O'Brien, M.F. Kinnaird and J. Supriatna, 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** (1998), pp. 89–106 10.1002/(SICI)1098-2345(1998)44:2 < 89::AID-AJP1 > 3.0.CO;2-S. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (14)

Schrader and Hammerschmidt, 1997 L. Schrader and K. Hammerschmidt, Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach, *Bioacoustics* **7** (1997), pp. 247–265. View Record in Scopus | Cited By in Scopus (47)

Snowdon, 2004 C.T. Snowdon, Sexual selection and communication. In: P.M. Kappeler and C.P. van Schaik, Editors, *Sexual Selection in Primates: New and Comparative Perspectives*, Cambridge University Press, Cambridge (2004), pp. 57–70. **Full Text** via CrossRef

Steenbeek et al., 1999 R. Steenbeek, P.R. Assink and S.A. Wich, Tenure related changes in wild Thomas's langurs II: loud calls, *Behaviour* **136** (1999), pp. 627–650 10.1163/156853999501496. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (22)

Taigen and Wells, 1985 T. Taigen and K. Wells, Energetics of vocalization by an anuran amphibian (*Hyla versicolor*), *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **155** (1985), pp. 163–170 10.1007/BF00685209. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (92)

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

Thierry, 2004 B. Thierry, Social epigenesis. In: B. Thierry, M. Singh and W. Kaumanns, Editors, *Macaque Societies*, Cambridge University Press, Cambridge (2004), pp. 267–294.

Thierry, 2007 B. Thierry, Unity in diversity: lessons from macaque societies, *Evolutionary Anthropology* **16** (2007), pp. 224–238 10.1002/evan.20147. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (10)

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

Tosi et al., 2003 A.J. Tosi, J.C. Morales and D.J. Melnick, Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys, *Evolution* **57** (2003), pp. 1419–1435 10.1111/j.0014-3820.2003.tb00349.x. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (73)

Vehrencamp, 2000 S.L. Vehrencamp, Handicap, index, and conventional signal elements of bird song. In: Y. Espmark, T. Amundsen and G. Rosenqvist, Editors, *Animal Signals: Signalling and Signal Design in Animal Communication*, Tapir Academic Press, Trondheim (2000), pp. 277–300.

de Vries, 1995 H. de Vries, An improved test of linearity in dominance hierarchies containing unknown or tied relationships, *Animal Behaviour* **50** (1995), pp. 1375–1389 10.1016/0003-3472(95)80053-0. **Article** | PDF (1232 K) | View Record in Scopus | Cited By in Scopus (175)

de Vries, 1998 H. de Vries, Finding a dominance order most consistent with a linear hierarchy: a new procedure and review, *Animal Behaviour* **55** (1998), pp. 827–843 10.1006/anbe.1997.0708. Abstract | PDF (234 K) | View Record in Scopus | Cited By in Scopus (141)

de Waal and Luttrell, 1985 F.B.M. de Waal and L.M. Luttrell, The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display, *American Journal of Primatology* **9** (1985), pp. 73–85 10.1002/ajp.1350090202. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (63)

Wagner, 1992 W.E. Wagner, 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** (1992), pp. 449–462 10.1016/0003-3472(92)90055-E. Abstract | **Article** | PDF (1078 K) | View Record in Scopus | Cited By in Scopus (48)

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

Wich and Nunn, 2002 S.A. Wich and C.L. Nunn, Do male 'long-distance calls' function in mate defense? A comparative study of long-distance calls in primates, *Behavioral Ecology and Sociobiology* **52** (2002), pp. 474–484 10.1007/s00265-002-0541-8. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (20)

Wich et al., 2003 S.A. Wich, D.J. van der Post, M. Heistermann, U. Möhle, J.A.R.A.M. van Hooff and E.H.M. Sterck, Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs, *International Journal of Primatology* **24** (2003), pp. 1251–1265 10.1023/B: IJOP.0000005991.97232.2a. **Full Text** via CrossRef | View Record in Scopus | Cited By in Scopus (11)