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The Vocal Repertoire of Barbary Macaques: A Quantitative Analysis of a Graded Signal System

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Abstract

The vocal behavior of Barbary macaques (*Macaca sylvanus*) was studied in an outdoor enclosure at Rocamadour, France. Ad libitum recordings were made across a broad array of socioecological contexts from 92 individually identified subjects from all age–sex classes. From the recordings, 8479 calls were sampled and submitted to a Fourier transform. A custom software program was used to determine 35 acoustic parameters describing the call in terms of its frequency and time dynamics. On these parameters a cluster analysis was used to examine the acoustic morphology of the Barbary macaque vocal repertoire. The analysis revealed a highly graded structure with intergraded variations between different clusters ('call types'). There were clear age-related preferences in usage of different clusters, but animals of all ages were potentially able to produce the whole array of call types. The major sex difference was a differential use of certain call types in specific situations. Despite a clear sex dimorphism in body size no significant sex differences in the acoustic structure of calls in adults was found. There were no unidirectional relationships between the acoustic structure of a call and the context in which it was uttered, although call usage was more specific in some contexts than in others. The results suggest that the major factor underlying the variation in acoustic structure reflect the internal state of the caller.

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Introduction

Communication systems can be distinguished on the basis of whether signals within the repertoire are 'graded' or 'discrete' (MARLER 1977). A graded signal system reveals continuous variation between signal types, i.e. there are no distinct boundaries to discriminate one signal type from another, whereas discrete repertoires consist of signals with no intermediates between signal types. Vocal repertoires composed of intergraded signals can be expected among those species with ready visual access to each other (MARLER 1976, 1977). Thus, intergradation is supposed to be more frequent in species less dependent on audible signals for their social regulation. On the other hand, vocal repertoires of species with far more visual restrictions, like squirrel monkeys, *Saimiri sciureus,* also reveal a

graded signal system with fluent transitions within as well as between call types (WINTER et al. 1966; SCHOTT 1975).

Several studies have been carried out on the vocal repertoires of different nonhuman primate species (hereafter 'primates'), for instance on rhesus monkeys, *Macaca mulatta* (ROWELL & HINDE 1962), squirrel monkeys (WINTER et al. 1966; SCHOTT 1975), vervet monkeys, *Cercopithecus aethiops* (STRUHSAKER 1967), Japanese macaques, *Macaca fuscata* (GREEN 1975, 1981), cotton-top tamarins, *Saguinus oedipus oedipus* (CLEVELAND & SNOW-DON 1982), and gelada baboons, *Theropithecus gelada* (AICH et al. 1990). Most primate repertoires are neither completely graded nor consist completely of discrete signals, but may be characterized as a mixture of graded and discrete signal structures (GREEN & MARLER 1979). Furthermore, vocal repertoires of the same species have been described both as graded and discrete. ROWELL & HINDE (1962), for instance, characterized the rhesus macaques' vocal repertoire as a graded system. In a later study, GOUZOULES et al. (1984) identified five distinct scream vocalizations during agonistic encounters, suggesting that the description of a signal system may depend on the level of analysis and the method applied.

Previous studies on the vocal communication of Barbary macaques, *Macaca sylvanus,* indicated that their vocal repertoire consists of a large array of highly variable calls (POHL 1984; HAMMERSCHMIDT et al. 1994a; TODT et al. 1995). The majority of their vocalizations reveal a noisy or compound acoustic structure. Based on the inspection of spectrograms, both the gradedness of the repertoire and the complex structure of the calls impaired a clear definition of call types. Even if it poses no problem to discriminate a high-pitched tonal scream from a low-frequency bark or grunt, an overview of a large variety of calls renders it difficult to establish boundaries between different classes of calls. These difficulties increase when a broad sample of vocalizations in different socioecological contexts and from different age–sex classes of callers are examined.

In the present investigation, we followed our computer-based multi-parametric approach used in former studies on Barbary macaques' vocalizations (e.g. HAMMER-SCHMIDT et al. 1994a; HAMMERSCHMIDT & TODT 1995; FISCHER et al. 1995) to examine the acoustic morphology of their vocal repertoire. To identify objective structures in the acoustic space of their vocalizations, we used a cluster analysis. Different cluster models created by the analysis can be examined in terms of improvement of their explanatory power (BACHER 1994). While more conventional approaches for establishing vocal repertoires are often guided by classification of calls according to their function or the context in which they were uttered (grouping 'alarm calls', 'contact calls', 'food calls', etc.), the cluster analysis does not rely on prior assumptions on the structure of the repertoire.

We will first present a method to identify clusters in the signal system of the species under study and then describe the general acoustic structure of the Barbary macaques' vocal repertoire. By examining call usage in different situations and age- and sex-related differences in call usage and in acoustic features, we aim to identify the major factors governing the variation in acoustic structure. In sum, we try to provide a comprehensive picture of the vocal repertoire of Barbary macaques using quantitative analyses to define some of the significant properties of the repertoire morphology. This approach should serve to derive testable hypotheses on the perceptual salience of acoustic features.

Methods

Study Animals and Study Site

We conducted this study on Barbary macaques living in an outdoor enclosure at Rocamadour, France (size: 15 ha). The enclosure is a visitor park where monkeys range freely while visitors are restricted to a path. Individuals are well habituated to human observers and are tattooed with an individual code on the inside of the thigh. The monkeys are provisioned with monkey chow provided in feeder huts, and with apples, grain, and seeds which are spread throughout the park. During the course of the study the population size increased from 174 animals in 1987 to 240 animals in 1993. For details on park management and history, see DE TURCKHEIM & MERZ (1984) and TODT et al. (1992).

Recordings and Acoustic Analysis

Recordings were taken between 1987 and 1993 as part of a number of studies on the monkeys' vocal communication (HAMMERSCHMIDT et al. 1994a; HAMMERSCHMIDT & TODT 1995; FISCHER et al. 1995). Vocalizations were recorded at a distance of 1–10 m with a Marantz cp 430 or a Sony WM DC6 cassette recorder and a Sennheiser directional microphone (KN3 power module and ME80 or ME88 recording head with Sennheiser windscreen) and transferred to a DAT tape (SONY TCD-D3) for storage. We visually inspected the recordings and sampled calls that were not disturbed by background noise for analysis using RTS 1.31 (Engineering Design, Boston).

The digitized calls were transformed in their frequency-time domain with SIGNAL 2.29 (Engineering Design, Boston), using a fast Fourier transformation (FFT) size of 1024 points. Depending on the frequency range of the calls we used a sampling frequency of 25 or 37.5 kHz, resulting in a frequency range of 10 or 15 kHz and a frequency resolution of 24 or 37 Hz. The time increment was 5 ms. The resulting frequency-time spectra were analysed with the software LMA 5.9 developed by Kurt Hammerschmidt. We used 35 acoustic parameters in the analysis which, in previous analyses of Barbary macaque vocalizations, had proven to be instructive (see Appendix). A description of this multiparametric approach is given in SCHRADER & HAMMERSCHMIDT (1997).

Cluster Calculations

To analyse the structure of the acoustic parameter space, we conducted a cluster analysis (method: k-means cluster) on the standardized values (z-scores) of the acoustic parameters. To assess the power of different cluster solutions, we calculated 29 cluster solutions (2–30 clusters) and assessed them separately according to a procedure described in BACHER (1994). In this procedure, the observed variation for each cluster solution is compared to the overall variation of the unpartitioned data set ('Zero-model'). We calculated two indices to assess the power of the different cluster solutions: (1) $Eta_{(k)}$ (Eq. 1), which reflects the relative reduction in variance by a given cluster solution. With a growing number of clusters $Eta_{(k)}$ increases successively. Therefore, it is mainly of interest to identify peaks in the course of $Eta_{(k)}$. (2) $Pre_{(k)}$ (Eq. 2), which represents the relative improvement in the reduction of variance compared to the previous solution. $SS_{in}(K)$: Sum of squares in the Kth Cluster; $SS_{in}(1)$: Sum of squares in the unpartitioned data set.

$$Eta_{(k)} \, s = 1 - \frac{SS_{in}(K)}{SS_{in}(1)} \tag{Eq. 1}$$

$$Pre_{(k)} = 1 - \frac{SS_{in}(K)}{SS_{in}(K-1)} \tag{Eq. 2}$$

Statistical Analyses

We sampled calls from 92 individually identified subjects, 40 males and 52 females. Some of these subjects were recorded in different years: seven males were recorded in two different years and two males in three different years; eight of the females were recorded in two different years and one female in three different years. The total number of calls in our analysis was 8479, including 1518 calls where the age and sex of the caller was known but the identity of the subject could not be determined. This data set was used to establish the cluster solutions and examine the usage of different call types in different contexts. For analyses regarding age- and sex related differences, only calls from individually identified subjects were used. Additionally, we removed calls from

subjects which were represented in multiple age-classes so that each subject was represented in one age-class only, reducing the number of calls in this data set to 6093. For the assessment of differences in acoustic parameters, we performed multivariate and univariate ANOVAs, and a Spearman rank-order correlation analysis using the mean value per individual and cluster. We also performed discriminant function analyses (DFA) to examine differences in calls between groups. The DFA compares multivariate patterns resulting from any interaction of variables (NORUŠIS 1993) and provides a classification procedure that assigns each case to its appropriate group (correct assignment) or to another one (incorrect assignment).

To assess the diversity of calling in different subcontexts we calculated the Simpson's diversity index D (BEGON et al. 1990) which integrates the number of different items in a sample and their abundance $(D = 1/ (\Sigma P_i^2)$, where P_i is the proportion of total calls in the ith cluster; $D = 1$ when all calls in one situation are assigned to the same cluster; D_{max} = total number of clusters. Thus we examined the variety of clusters occurring in one call bout (i.e. all consecutive calls given in one specific situation) in relation to the total number of calls in this bout. We calculated D for the calls of 26 call bouts of 12 females (n = 492 calls with a mean of 18.9 calls per bout, ranging from 10 to 38), and used the mean for each individual in a Mann–Whitney U-test to assess the difference in call diversity in the subcontexts. All statistical analyses were done with the statistical package SPSSWIN 6.1.2.

We established 10 social contexts and divided them into 39 sub-contexts:

1. 'Mating' (main context): calls given in the mating season in the subcontexts copulation, attempted copulation, interrupted copulation, and after copulation (see also TODT et al. 1995);

2. 'Infant care': calls emitted by the care-giver during infant care (both maternal & alloparental care; SMALL 1990; PAUL et al. 1996): infant is quiet; infant screams/tries to get away from the care-giver; infant is taken away from care-giver by a third party;

3. 'Quiet situation': resting, foraging, locomotion;

4. 'Agonistic situations': fight in a distance, group fight, male 'actor' in a male–male fight, male 'target' in a male–male fight, 'actor' in situations other than male-male fights, 'target' of aggression by an adult male, 'target' of an adult female, 'target' of a juvenile, after agonistic encounter;

5. 'Disturbance': disturbance by the observer, by park staff, by a dog, by a snake (FISCHER et al. 1995);

6. 'Sleeping cluster formation' (HAMMERSCHMIDT et al. 1994b): subject is alone, with juvenile, attempts to achieve contact with a group, in body contact with a group;

7. 'Infant in care': infant is with the mother, with a female, with a male, with a juvenile (see above);

8. 'Play': solitary play, rough-and-tumble play (PREUSCHOFT 1992);

9. 'Contact': making or breaking contact with group of subjects huddled on the ground, during contact with a huddle;

10. 'Infant search': calls recorded from females whose dead infant was taken away by the park staff, whose infant was with another individual in sight or out of sight of the mother. Females appeared to be looking for their infants or were trying to retrieve their infants from alloparental care.

Furthermore we noted the detailed behaviour of the subject. Finally, we established five age-classes: 1. infants up to the age of 1 yr; 2. young juveniles of 1 to 2 yrs; 3. elder juveniles of 2 to 3.5 yrs; 4. subadults: females of 3.5 to 5 yrs and males of 3.5 to 7 yrs; 5. adult females older than 5 yrs and adult males older than 7 yrs of age.

Results

General Structure of the Vocal Repertoire

Fig. 1 presents the course of $Eta_{(k)}$ and $Pre_{(k)}$ in relation to the different numbers of clusters that we calculated to determine the most powerful cluster solution. Starting with a reduction of 24.9% at the 2-cluster solution, the Eta-coefficient showed a continuous increase with a local peak at the 7-cluster solution and a minor peak at the 16-cluster solution. Beside the 4-cluster solution, further high Pre-values occurred at the 5-, 7-, 9-, 16-, and 18-cluster solutions (Fig. 1). The high values of the 9- and 18-cluster solution depended on the negative values of previous solutions. In accordance, there was no increase in Eta. In viewing both Eta and Pre, the 2-, 4-, 7- and 16-cluster solutions were considered to be appropriate to partition the data set into meaningful clusters.
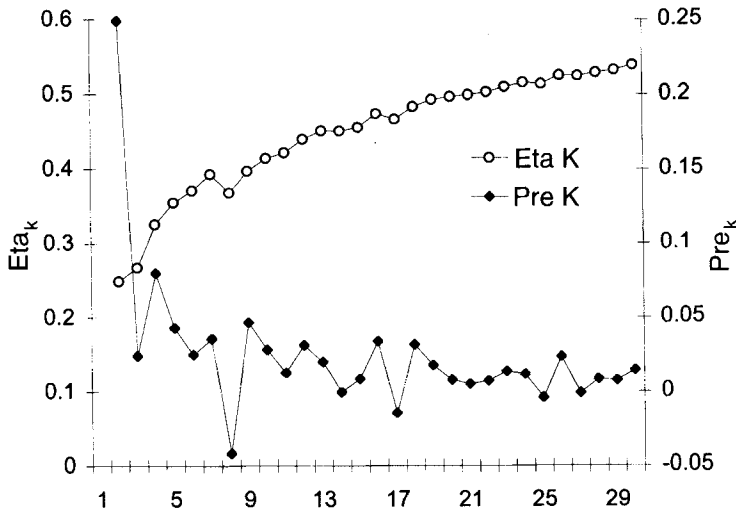
Fig. 1: Changes in Eta(k) and Pre(k) in relation to the different cluster solutions. Based on these coefficients, the 4-, 7-, and 16-cluster solution were considered to be most appropriate to partition the data set into different clusters

With the exception of the 2-cluster solution, none of the three other solutions was clearly superior. The 4-cluster solution showed the second highest Pre-value (0.08) but there was a constant increase in Eta until the 7-cluster solution. The 16-cluster solution showed a further increase in Eta, but the newly established clusters were less clearly separated. Additionally, this solution created three clusters with 2 or 3 cases only, which were partly responsible for the higher Eta-value. Therefore we decided to choose the 7-cluster solution because it provided a balance between the cohesion within clusters and the isolation between clusters.

Fig. 2 shows the changes in the distribution of calls among the different clusters for the 2-, 4- and 7-cluster solution. The calls of cluster 1 and 2 in the 2-cluster solution remained well separated. The calls from cluster 1, mainly noisy low-pitched barks or grunts were assigned to clusters A, B, C, and D, depending on their frequency range and pitch (see also Fig. 3, 4). The calls from cluster 2 (mainly tonal high-pitched screams) were split into the clusters E, F, and G. Clusters E and F differed mainly in their frequency range. Calls in cluster G were well separated by their high modulation in call amplitude (Fig. 3, 4). Minor regrouping occurred between clusters D and E: some calls from cluster 1 in the 4-cluster solution were assigned to cluster E, and a small number of calls from cluster 2 were assigned to cluster D.

Fig. 3 shows the discrimination of the clusters by means of a discriminant function analysis. All clusters (except cluster G) could be clearly discriminated by the first two discriminant functions. Fig. 4 shows spectrograms of calls which were assigned closest to the group centroid for each cluster, i.e. to the group mean.
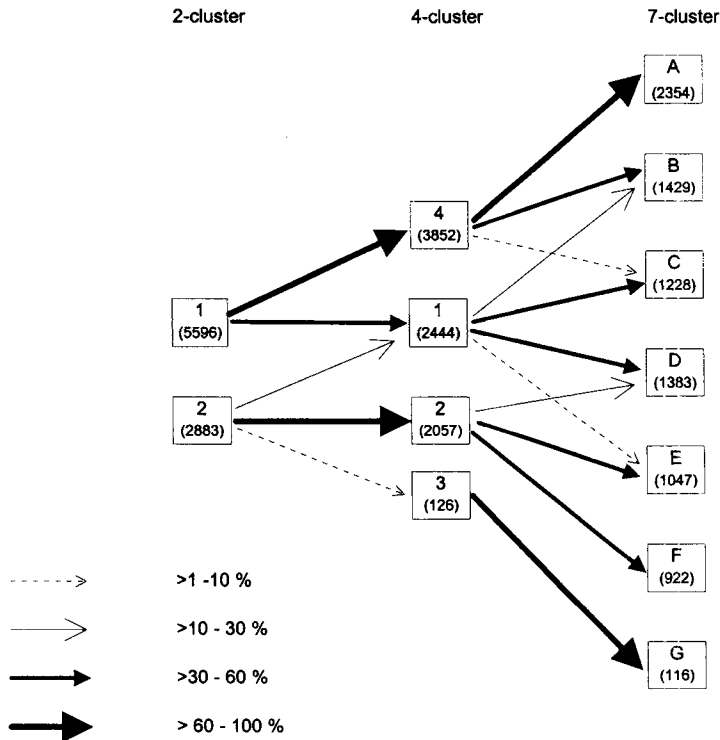
Fig. 2: Size of the arrows (see key) represents the relative distribution of calls from clusters in the preceding cluster solution to clusters in the following cluster solution. Values in brackets give the number of calls in the cluster

Usage of Call Types

The relative frequency of cluster usage revealed age-related differences. Infants and 1-yr-old animals (age-classes 1 and 2) mainly uttered the call types D, E, and F. Juveniles (age-class 3) mainly used call types C and D, with the exception that males also had a preference for A. However, there were only few individuals represented in this age-class. Subadults and adults (age-classes 4 and 5) mainly uttered call types A, B, and C. However, subadults also used a fair amount of D and E calls. In general there was no difference in call usage between males and females. In sum, we observed a shift from a frequent use of scream-type calls and higher-pitched grunt-like calls in young animals to the use of low-frequency grunts in adults.

Age- and Sex-related Differences in Acoustic Parameters

A MANOVA revealed significant age-related differences in acoustic features in all clusters except cluster E (Table 1). We then determined the correlation of those parameters which exhibited significant differences in relation to age. It turned out that four parameters (mean central frequency, mean local modulation of central frequency, mean 1st dominant
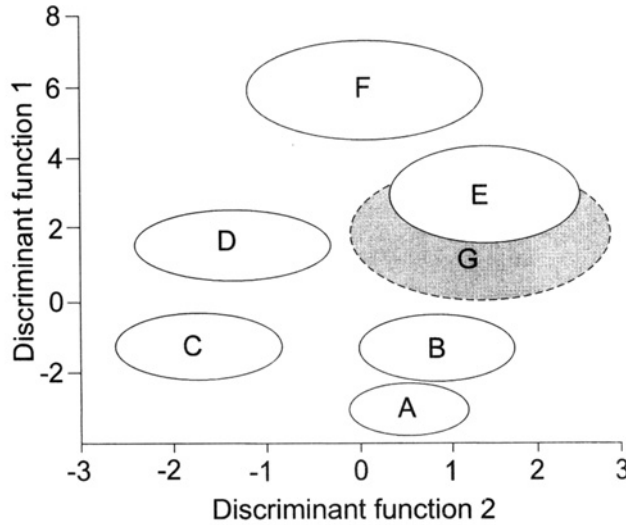
Fig. 3:   Arrangement of the clusters established by the 7-cluster solution in the acoustic space. Circles are spanned by the $\bar{X} \pm$ SD for the first two discriminant functions. Function 1 showed the highest correlation with the call parameters 'mean' and 'minimum of the central frequency', 'mean peak frequency' and 'mean of the 1ˢᵗ dominant frequency peak'. Function 2 correlated best with the 'mean frequency range', 'mean range of the 1ˢᵗ formant-like structure', and 'intercept of the general frequency trend'. All clusters (except cluster G) could be clearly discriminated by the first two discriminant functions; a third discriminant function was necessary to discriminate between clusters E and G

frequency band, and mean local modulation of 1st dominant frequency band) showed a negative correlation, i.e. with increasing age, pitch and modulation were decreasing (Table 1).

To examine differences in acoustic structure between the sexes, we analysed those clusters in which a sufficient number of adult subjects of both sexes were represented

Table 1:   Multivariate age-related differences within clusters and Spearman rank-order correlation coefficients for age-related differences in four acoustic parameters

Cluster	n	Wilk's F	p	cf mod	cf mean	1st dfb mod	1st dfb mean
A	61	1.51	<0.05	−0.33*	−0.08	−0.24	−0.03
B	66	1.46	<0.01	−0.50*	−0.48	−0.30	−0.30
C	72	1.37	<0.05	−0.24	−0.23	−0.37*	−0.37*
D	71	1.57	<0.01	−0.54*	−0.50*	−0.48*	−0.51*
E	49	0.93	ns	−0.53*	−0.46*	0.12	−0.42*
F	42	1.51	<0.05	−0.62*	−0.24	−0.19	−0.19
G	27	2.2^{1}	<0.05	−0.65*	−0.72*	−0.77*	−0.57*

^{1}age = 1,2,5; cf: central frequency, 1st dfb: 1st dominant frequency band, mod: modulation; *p < 0.05, sequential Bonferroni correction.
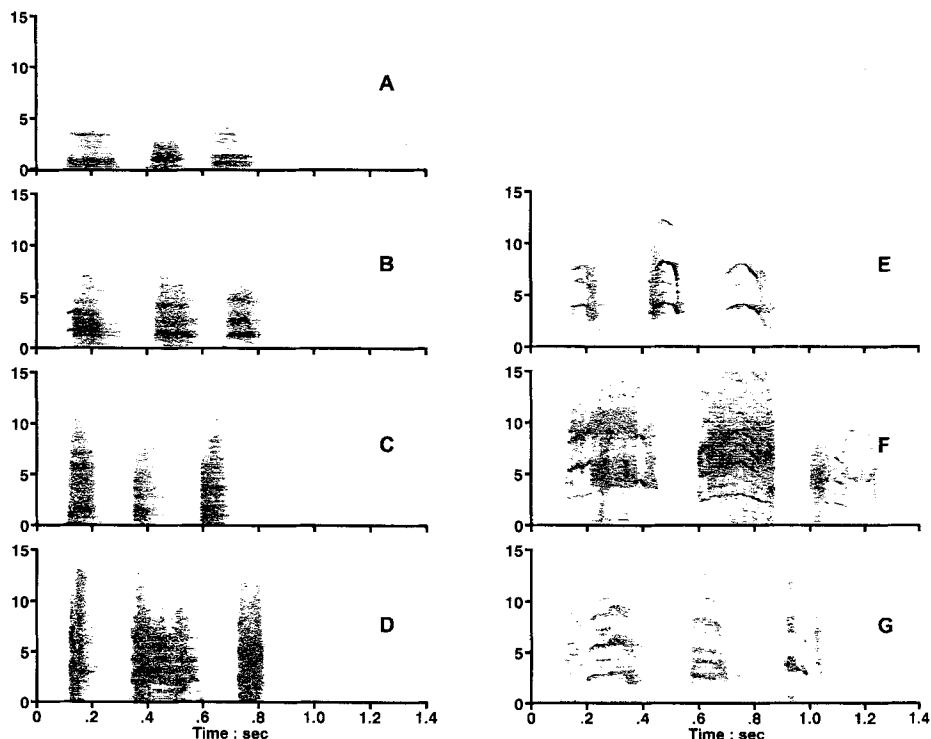
Fig. 4: Spectrograms of calls representing the seven clusters ('call types'). For each graph, three call exemplars recorded from three different subjects which showed the smallest distance to their respective cluster centres were chosen. Frequency range: 15 kHz

(clusters A, B, and C). A MANOVA revealed significant differences in clusters A and C (cluster A: n = 9 males, 20 females; Wilk's exact $F_{17,11} = 18.43$, p < 0.001; cluster C: n = 9 males, 19 females, Wilk's exact $F_{17,10} = 2.82$, p < 0.05). However, these sex differences might in fact be due to contextual differences, i.e. male and female calls might stem from different situations. Therefore, we performed an additional analysis only on those calls which were uttered in 'quiet situations'. Only cluster B provided a sufficient number of subjects to perform a meaningful analysis. Within this cluster, there were no significant multivariate differences in the acoustic features between males and females (n = 6 males, 13 females; Wilk's exact $F_{12,6} = 0.56$, ns).

Context-related Differences

Fig. 5 shows the relative frequency of calls of the various clusters observed in the different contexts. Since the contexts were to some degree age- and sex-specific, the distribution of the use of the different call types corresponded to the one observed for the different age-classes. For instance, calls recorded in the context 'in alloparental care' were recorded from infants, and calls recorded during sleeping cluster formation were almost exclusively recorded from young juveniles. In these contexts, subjects mostly used calls of

	Cluster							N calls	N subjects
	A	B	C	D	E	F	G		
mating (m)	●	●	●	●	●	●	●	187	5
mating (f)	●	●	●	○	○	○	○	1296	14
infant care	●	●	●	●	●	○	○	147	9
quiet situation	●	●	●	●	●	○	○	486	33
agonistic sit.	●	●	●	●	●	●	●	3286	66
disturbance	●	●	●	●	●	○	○	373	12
sleeping cluster	○	●	●	●	●	●	●	417	8
infant in care	○	●	●	●	●	●	●	1445	27
play	●	●	●	●	●	●	○	327	18
contact	●	●	●	●	●	●	●	111	12
infant search (f)	●	●	●	●	●	○	○	404	7

Fig. 5: Cluster usage in the different main contexts, total number of calls in each cluster, and number of calls and subjects represented in each context (m, males; f, females). Circles represent 0–<1%, 1–<10%, 10–<30%, 30–<60%, 60–100%. Total n = 8479 calls

the clusters D, E, and F. In general, there was no simple relation between context and the use of specific call types. All call types were observed in several contexts, and in all the contexts, several call types were used. In some contexts, for instance during copulation or when females were in search of their infants, there was a higher specificity in the call type usage. Splitting contexts into finer subcontexts did not change the result in a fundamental way (see below).

To accomplish a more detailed insight into differences in call usage in different subcontexts, we compared call usage in 12 females which provided a sufficient number of calls within a given situation. We examined the relative assignment of calls to the different clusters for each call bout for two subcontexts: during copulation and when the female was the target of aggression by an adult male. Call usage was significantly more diverse in the agonistic situation than during copulation (copulation: 1.38 $\pm$ s 0.13 ($\bar{X} \pm$ s SD), chased 2.82 $\pm$ s 0.37; $n_1 = 6$, $n_2 = 6$, U = 3, p < 0.05). Calls uttered in the mating context were mainly assigned to cluster A (81.4%) and B (14.7%). Calls used in agonistic situations were assigned to cluster A (24.7%), B (19%), C (31%), D (15.8%), and E (5%).

Discussion

The aim of our study was to describe the general acoustic structure of the vocalizations of Barbary macaques. The results of the cluster analysis showed that the Barbary macaques'

vocal repertoire is a highly graded signal system ranging from low-frequency grunt-like calls to high-pitched screams. Within this continuously distributed acoustic space some acoustic configurations were observed more frequently than others, i.e. they emerged as different clusters and could be defined as 'call types'. Due to this probabilistic and graded structure of the repertoire, different cluster solutions were appropriate to partition the data set. Thus, it was to a certain extent a pragmatic decision to choose the 7-cluster solution for closer examination.

It is unlikely that the cluster analysis did not reveal discrete call types due to methodological problems. For instance, in a study of the vocal development in young rhesus macaques in which the same methodological approach was used, coo calls could be clearly separated from other call types (HAMMERSCHMIDT & NEWMAN 1996). SCHRADER (1996) also used a cluster analysis in a similar analysis of different call types in domestic pigs, *Sus scrofa domestica*. We conclude therefore that the cluster analysis would have revealed isolated call types if they were present.

There are few comprehensive studies on the vocal repertoires of other macaque species, for instance GREEN (1975) on Japanese macaques or PALOMBIT (1992) on long-tailed macaques, *Macaca fascicularis*. Most other studies addressing macaque vocal behaviour dealt with more specific aspects, e.g. the use of 'food calls' in toque macaques, *Macaca sinica* (DITTUS 1984) or the variation in recruitment screams in pigtail macaques (GOUZOULES & GOUZOULES 1995). From what is presented in such reports we assume that most macaque repertoires are graded, but reveal considerable interspecific variation. However, due to the lack of detailed information it remains difficult to assess the influence of phylogenetic relatedness or habitat structure on the repertoire morphology. Nonetheless, it seems that Barbary macaques, the only African macaques, use considerably more harsh and noisy vocalizations and have a very limited use of 'coo calls' compared to the Asian macaques. This also seems to be true in comparison with another terrestrial macaque, the stump-tailed macaque, *Macaca arctoides* (LILLEHEI & SNOWDON 1978).

Age- and Sex-related Variations

The major age-related difference was that younger animals more frequently used calls from high-frequency scream type clusters (cluster E and F), whereas older animals most often used lower frequency grunt-like calls (clusters A, B, and C). However, occasionally adults produced screams that were similar to the ones produced by infants and, likewise, young animals produced low-frequency calls that resembled those of adults, indicating that animals of all age-classes are potentially able to produce the whole array of call types of the vocal repertoire (see also HAMMERSCHMIDT et al. 1994a). In this former study, we examined variations in acoustic parameters across the entire range of calls and found that the major age-related shift was a decline in the peak frequency and in the maximum frequency range with increasing age. It is of interest that these parameters were crucial for characterising the different clusters in our current analysis.

Younger animals were found to produce calls with a higher local modulation of the central frequency and the 1st dominant frequency band, which could be related to a less well developed vocal motor control in younger animals. The mean central frequency and the 1st dominant frequency band decreased with increasing age. This decrease in pitch

could be explained by an increase in body size and, correspondingly, in the size of the larynx (FITCH & HAUSER 1995). Surprisingly, we did not find a significant difference between the sexes in the present study despite a considerable sex dimorphism in body size (males are up to one third heavier than females; PAUL 1984). Also, other acoustic parameters which may reflect differences in the size of the vocal tract, i.e. parameters characterising the 'formant dispersion' (FITCH, in press) did not reveal any differences between the sexes. One explanation for this lack of sex difference in acoustic structure might be that the variation caused by changes in internal state overrides the variation caused by a difference in body size.

Assignment to Contexts

In general, there were no unidirectional relationships between call structure and the context in which a certain call was used. Even splitting the contexts into finer subcontexts did not change the results in a fundamental way. Additionally, a high call diversity in specific situations indicates that the animal's assessment of a situation may change within very short time periods. Thus, the major factor underlying variation in call structure seems to be the expression of some internal variables (TODT 1996). This finding agrees with DARWIN's hypothesis (1872) that mammalian vocalizations mainly reflect the internal state of the caller and that the gradations of their vocal repertoires correspond to the graded changes in internal states (see also NEWMAN & GOEDEKING 1992). A self-stimulation study on squirrel monkeys (JÜRGENS 1979) confirmed this view. Within different call categories JÜRGENS found a correlation between the degree of aversiveness and the variation in certain call parameters.

Nevertheless, in some cases, specific relationships between context and certain vocalizations exist. An example are copulation calls, which consist of a series of short grunt-like units (see also TODT et al. 1995). In this case, the temporal dynamics of the vocalizations seem to mediate the context-specific information, as the acoustic structure of the single units apparently is the same in mating or non-mating situations.

Despite the high variability of calls uttered in different contexts, some vocalizations may still convey very specific information. Calls given in response to disturbances in the monkeys' surroundings, for instance, were not classified as one single call type based on their parametric cues. Yet Barbary macaques responded to the playback of alarm calls with escape responses, i.e. the information encoded in the acoustic features was sufficient to elicit an appropriate response (FISCHER et al. 1995). That is, the conspecific perceivers of the signal were able to extract salient features from the signal that enabled them to identify the call as an alarm call. In a separate study, FISCHER (in press) tested the categorisation of intergraded signals given in response to two different possibly threatening stimuli. These experiments showed that subjects partitioned the gradual transition between calls into two categories, suggesting that they discriminated among calls according to their call meaning.

It seems likely that Barbary macaques in general are equipped with perceptual mechanisms to partition the continuous acoustic structure into biologically significant categories. This might be mediated by the existence of acoustic 'prototypes' which may be genetically predisposed or acquired. Graded repertoires that are associated with perceptual mechanisms to partition the acoustic stream into functionally meaningful categories have

the potential to encode considerably greater amounts of information than discrete rep-
ertoires (HAUSER 1996). Clearly, further perceptual experiments are required to test
whether the acoustic categories established by our current study correspond to what the
animals themselves perceive as meaningful.

In sum, we conclude that a broad quantitative analysis as presented here is necessary
to reveal the complex structure of a primate vocal repertoire such as the vocal repertoire
of Barbary macaques. This detailed knowledge is helpful to derive hypotheses about the
factors underlying call production, call usage and the perceptual mechanisms required to
process the information encoded in the calls.

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Appendix

1. Call parameters calculated from the original frequency-time spectra: start, end, minimum, maximum, and mean central frequency (Hz); slope 1 (from start to maximum frequency) and slope 2. (from maximum frequency

to end) of central frequency (Hz/ms); location of the maximum central frequency relative to the total call duration [(1/duration)*location]; mean local modulation of central frequency (Hz); start, end, minimum, maximum, and mean peak frequency (Hz); location of the maximum peak frequency; call duration (ms), mean duration of amplitude gaps (ms); percentage of time the fundamental frequency can be calculated, percentage of time the calls are noisy (both calculations are based on an autocorrelation function); location of the maximum difference in call consistency (based on the correlation coefficient of successive call segments).

2. The frequency-time spectrum was filtered using two different weighted functions to enhance the signal-to-noise ratio and to differentiate between global and local energy peaks. The spectrum weighted with the first function was used to describe the course of the local frequency peaks, which, in tonal vocalizations, correspond to the fundamental frequency (F0) or its harmonics. Call parameters calculated from the 1st weighted frequency-time spectra: 1st dominant frequency peak: start, end, minimum, maximum, and mean frequency (Hz); location of the maximum and minimum frequency; mean local modulation. (Hz); slope and intercept (Hz) of the general frequency trend. The spectrum weighted with the second function was used to describe formant-like structures and the frequency range: mean range of the 1st, 2nd, and 3rd formant-like structures (fls) (Hz), amplitude peak of the 1st fls (relative in mV); mean frequency range (Hz).