

Department of Biology, University of Pennsylvania, Philadelphia; Department of Psychology, University of Pennsylvania, Philadelphia; Deutsches Primatenzentrum, Abteilung Neurobiologie, Göttingen

Acoustic Features of Female Chacma Baboon Barks

Julia Fischer, Kurt Hammerschmidt, Dorothy L. Cheney & Robert M. Seyfarth

Fischer, J., Hammerschmidt, K., Cheney, D. L. & Seyfarth, R. M. 2001: Acoustic features of female chacma baboon barks. *Ethology* **107**, 33–54.

Abstract

We studied variation in the loud barks of free-ranging female chacma baboons (*Papio cynocephalus ursinus*) with respect to context, predator type, and individuality over an 18-month period in the Moremi Game Reserve, Botswana. To examine acoustic differences in relation to these variables, we extracted a suite of acoustic parameters from digitized calls and applied discriminant function analyses. The barks constitute a graded continuum, ranging from a tonal, harmonically rich call into a call with a more noisy, harsh structure. Tonal barks are typically given when the signaler is at risk of losing contact with the group or when a mother and infant have become separated (contact barks). The harsher variants are given in response to large predators (alarm barks). However, there are also intermediate forms between the two subtypes which may occur in both situations. This finding is not due to an overlap of individuals' distinct distributions but can be replicated within individuals. Within the alarm bark category, there are significant differences between calls given in response to mammalian carnivores and those given in response to crocodiles. Again, there are intermediate variants. Both alarm call types are equally different from contact barks, indicating that the calls vary along different dimensions. Finally, there are consistent, significant differences among different individuals' calls. However, individual identity in one call type cannot directly be inferred from knowledge of the individuals' call characteristics in the other. In sum, the barks of female baboons potentially provide rich information to the recipients of these signals. The extent to which baboons discriminate between alarm and contact barks, and classify calls according to context and/or acoustic similarity will be described in a subsequent paper.

Corresponding author: Julia Fischer, Max-Planck Institute for Evolutionary Anthropology, Inselstr. 22, D-04103 Leipzig, Germany. E-mail: fischer@eva.mpg.de

Introduction

In Darwin's (1872) view, animal signals should be understood as predominant expressions of emotions (see also Marler 1977a, 1992; Owings & Morton 1998). However, a number of the vocalizations given by non-human primates are functionally referential, in the sense that listeners can extract quite specific information about objects or events in the environment based solely or largely on a call's acoustic features. In the case of some calls, acoustic structure is strongly correlated with a specific object or event. The alarm call given by vervet monkeys (*Cercopithecus aethiops*) in response to mammalian carnivores, for example, is acoustically different from the call given in response to eagles (Struhsaker 1967; Seyfarth et al. 1980; Owren & Bernacki 1988). Moreover, although the rate of delivery and amplitude of alarm calls in some species may change according to the immediacy of danger, their overall acoustic structure remains the same (e.g. vervet monkeys, Seyfarth et al. 1980; ring-tailed lemurs *Lemur catta*, Macedonia & Evans 1993; Barbary macaques, *Macaca sylvanus*, Fischer et al. 1995). In the case of other calls, however, acoustic structure appears to be more closely correlated with the signaler's affective state, presumably a measure of perceived risk or fear (e.g. ruffed lemurs, *Varecia variegata*, Macedonia 1990; ground squirrels, *Spermophilus* sp., Owings & Virginia 1978; Leger et al. 1979).

Current theory suggests that acoustically distinct alarm calls should evolve when animals confront different predator species whose hunting strategies require different modes of escape (Marler 1965, 1967; Cheney & Seyfarth 1990; Macedonia & Evans 1993). Moreover, in order to reduce ambiguity over long distances, the calls should be acoustically discrete. According to this view, call function determines both the referential specificity of each vocalization and the number of calls within a species' repertoire. The alarm calls of vervet monkeys provide strong support for this hypothesis. Vervets encounter a variety of different predators that hunt in different ways and require different escape strategies. Presumably as a result, the monkeys possess several acoustically distinct alarm calls, each of which elicits a different, adaptive response (Struhsaker 1967; Seyfarth & Cheney 1980). The loud barks given by female baboons, however, present a challenge to this hypothesis.

Female baboons' loud barks constitute a graded continuum, ranging from tonal, harmonically rich calls into calls with a more noisy, harsh structure. The more tonal contact barks (Hall & DeVore 1965; Byrne 1981; Cheney et al. 1996; Rendall et al. 2000) are typically given when the signaler is at risk of losing contact with the group or when a mother and infant have become separated. Contact barks are typically given in bouts. Often, animals climb into trees or up termite mounds while calling and scanning the area (see Cheney et al. 1996; Rendall et al. 2000 for a more complete description of the context of contact barks).

The harsher variants, 'harsh' or 'shrill alarm' barks (Hall & DeVore 1965), are given in response to large predators such as lions (*Panthera leo*) and leopards (*P. pardus*), as well as to snakes, crocodiles (*Crocodilus niloticus*), and the sudden appearance of minor predators such as hyenas (*Crocuta crocuta*) and wild dogs

(*Lycaon pictus*). The most common adult male alarm call is a loud, two-syllable vocalization, called a wahoo (Hall & DeVore 1965; Byrne 1981). Males also give wahoos during inter-group encounters, when herding females, and when they have lost contact with the group. The first part of the call, the 'wa', is similar to the bark of females. The second syllable, or 'hoo' has a lower amplitude and often a lower fundamental frequency (J. Fischer, K. Hammerschmidt, D. L. Cheney & R. H. Seyfarth, unpubl. data). Juvenile and infant baboons also give alarm calls that, apart from some age-related acoustic differences such as a substantially higher fundamental frequency, acoustically resemble the barks of females.

Although some variants of female baboons' alarm and contact barks are relatively easy to distinguish by ear, others are acoustically intermediate and difficult to assign to a particular category. They therefore challenge the view that functionally different calls should be acoustically distinctive. Below, we present a detailed acoustical analysis of both bark variants. We first explore the acoustic differences between contact and alarm barks; we then examine the extent to which alarm barks given in response to different predator types (lions vs. crocodiles) also show consistent acoustic variation. Finally, we focus on individual variation within and between contexts, to investigate the problems associated with the simultaneous recognition of call types and individual identity. Our aim is to formulate hypotheses about the potential information content available to the receivers of these signals. Results of playback experiments to test these hypotheses will be described in a subsequent paper.

Methods

Study Site and Subjects

The study site lies in the Moremi Wildlife Reserve in the Okavango Delta, a huge inland delta fed by the Okavango river. Yearly rainfall in Angola causes the Okavango and its tributaries to rise and flood the grasslands. Only slightly elevated patches of woodland, or 'islands', which range in size from less than one to hundreds of hectares, remain uncovered (Hamilton et al. 1976; Ross 1987). During the flood, the baboons ford the floodplains to travel from one island to the next.

The average size of a baboon troop's home range in the area is 450 ha (range 210–650 ha; Hamilton et al. 1976). The study group, group C, has been observed more or less continuously for more than 20 years. The matrilineal relatedness of all natal animals is known. The animals are fully habituated to observers on foot and can be approached up to 1 m. There are a number of comprehensive studies on the social behavior (Hamilton et al. 1976; Bulger & Hamilton 1988; Hamilton & Bulger 1990; Bulger 1993; Silk et al. 1999), as well as on the vocal communication of this population (Cheney et al. 1995, 1996; Palombit et al. 1997; Seyfarth & Cheney 1997; Cheney & Seyfarth 1999; Rendall et al. 1999). During the period of this study, group size ranged from 79 to 84 subjects, including 25 mature females.

Vocal Recordings and Behavioral Observations

We recorded vocalizations ad libitum with a Sony WM TCD-100 DAT recorder and a Sennheiser directional microphone (K6 power module and ME66 recording head with MZW66 pro windscreen) during an 18-month period between Jan. 1998 and June 1999. Whenever a female within earshot started calling, we approached that subject and attempted to record her calls. Any information regarding caller identity, identity of and distance to subjects in the vicinity, predator type, predator behavior, and predator distance were spoken onto the tape. At first, we aimed for an 'all-occurrences sampling scheme' (as far as this is possible in the field where subjects are often hundreds of meters apart). However, after about 6 mos we suspended recordings of three subjects from whom we had already gathered at least 40 high-quality recordings. For the acoustic analysis, we used only calls given at a distance of approximately 5–15 m from the microphone because some acoustic parameters can be influenced by signal transmission over large distances. We measured call amplitude (A-weighting) with a Realistic Sound Level Meter, Radio Shack, Fort Worth, Texas (accuracy ± 2 dB(A) at 114 dB(A) SPL). Only calls whose context could be determined unambiguously were subjected to acoustic analysis. Calls classified as contact barks were calls that were recorded when the signaler was visually separated from the group, either alone or with a small party of other animals, or when she had apparently lost contact with her infant. Calls classified as alarm barks were recorded when the signaler had apparently detected a predator (see Results).

Data on adult female bark rates were gathered during 64 observational hours between Jan. and May, 1998 and during 58 observational hours in Apr. and May of 1999. Data collection began in the early morning when the group left its sleeping site and embarked on its daily travel. Caller sex and age class was initially decided by call characteristics; as far as possible a second observer ascertained caller identity. To obtain an estimate of call intervals, we measured the time between calls to the nearest second, based on the readings from the DAT-recorder. Statistics of call intervals are based on a total of 449 inter-call intervals from 14 females for contact barks and from 11 females for alarm barks.

Acoustic Analysis

First, we visually inspected and sampled calls that were not disturbed by background noise (i.e. bird song, other animals calling) at a sample frequency of 11 024 Hz using RTS (Engineering Design, Belmont, MA; Beeman 1996) or Cool Edit (Syntrillium, Phoenix, AZ). Next, we used the SIGNAL sound analysis system (Engineering Design, Belmont, MA; Beeman 1996) to conduct a fast Fourier transform (1024-pt FFT; time step: 3 ms; frequency range: 4400 Hz, frequency resolution: app. 11 Hz).

We submitted the resulting frequency time spectra to a custom software program (LMA 8.4) developed by Kurt Hammerschmidt, which extracts different sets of call parameters from acoustic signals (Hammerschmidt 1990). Below, we briefly

describe the underlying principle for the different groups of measurements. A list of the calculated parameters is given in the Appendix.

We first calculated an autocorrelation function for every time segment in a given call. Depending on the number of peaks and the periodicity of the autocorrelation function, each time segment was classified as noisy (no peaks could be detected), complex (some peaks could be detected, but they were not periodic), or tonal (peaks were periodic). We then determined the percentage of time segments in a given call, which were noisy or complex (the percentage of tonal segments was not considered in the present analysis). If a time segment was classified as tonal, we determined the fundamental frequency. We then derived the maximum and the median value of the fundamental frequency across all time segments within a given call. Consequently, measures of the fundamental frequency are not available for all calls.

Secondly, we measured the statistical distribution of the frequency amplitudes in the spectrum (DFA). These values give the frequency at which the amplitude distribution in the spectrum reaches the first and second quartile of the total distribution, respectively.

Thirdly, we calculated a set of parameters describing the first three dominant frequency bands (DFB). The dominant frequency bands are characterized by amplitudes that exceed a given threshold in a consecutive number of frequency bins. Note that the numbers of the DFBs count from the lowest frequency up; the 1st DFB is not necessarily the DFB with the highest amplitude. In the tonal barks of chacma baboons, the 1st DFB corresponds to the fundamental frequency and the 2nd and 3rd DFB to the first and second harmonics. In addition to the mean and maximum values for these structural parameters, we estimated the local and global modulation of the 1st DFB for the entire call. The calculation of the local modulation is based on the differences between the course of the dominant frequency band and the smoothed curve. The global modulation estimates the differences between the course of the DFB and the regression line.

Fourthly, we determined the global energy distribution in the calls. In addition to the frequency range of the frequency amplitude, we calculated parameters which describe the main energy peaks in more detail. Fifthly, we specified the modulation of the peak frequency (PF), the frequency with the highest amplitude in a certain time segment. Finally, we determined the call duration. A description of the various algorithms is given in Schrader & Hammerschmidt (1997).

Additionally, we conducted a Linear Prediction Coefficient (LPC) analysis using SoundScope (GW Instruments, Somerville, MA). LPC analysis is an alternative to fourier transform for describing the spectrum of a signal segment (Owren & Linker 1995). For this analysis, we selected a 100-ms time segment of a tonal part of the call with a nearly constant fundamental frequency. We calculated 10 LPC-coefficients from a 4098 pt FFT spectrum. In this analysis, we used the frequency of the peak of the first formant (filtering frequency). We also determined the difference in frequency of the first and second formant, and the amplitude ratio between the first and second formant. However, a second formant could not be determined for all calls, resulting in a number of cases with missing values. (For a tutorial on

the sound production of animal vocalizations, see Fitch & Hauser 2000). Lastly, we inspected spectrograms for indications of the occurrence of non-linear phenomena (Wilden et al. 1998).

Statistical Analysis

We used a discriminant function analysis to identify differences in vocalizations between contexts and among individuals. Discriminant function analysis identifies a linear combination of quantitative predictor variables that best characterize the differences among groups (Bortz 1993). Variables are combined into one or more discriminant functions. Variables that fail a tolerance test, i.e. are an almost linear combination of other variables, do not enter the analysis. The discriminant function analysis establishes $n - 1$ discriminant functions, where n is the number of groups (e.g. contexts or individuals) in the analysis.

The discriminant function analysis provides a classification procedure that, based on the discriminant function, assigns each call to its appropriate group (correct assignment) or to the other group (incorrect assignment). For external validation, we used a 10-fold cross-validation in which roughly 90% of the data are selected randomly to calculate the discriminant functions and the remaining 10% of cases are used for classification. This procedure is iterated 10 times. For smaller sample sizes, we used the 'leave-one out' classification procedure, in which call assignment is based on all calls in the analysis with the exception of the one to be classified.

The amount of correct classification is not affected by repeated measures. However, it may be influenced by the number of variables in the analysis and the ratio of the number of variables to the number of cases in the analysis (Bortz 1993). In this analysis, we entered all variables simultaneously. In this way, the discriminant model is essentially based on all information available. However, this 'direct method' is much more susceptible to an unfavorable ratio of the number of cases in the smallest sample vs. the number of parameters used. Nonetheless, Pimentel & Frey (1978) advocate the use of the direct method over the stepwise procedure because the latter relies on the predictor variables alone and discards potentially meaningful variation in other variables. For follow-up tests of single acoustic parameters, we used the Wilcoxon signed-rank test when a set of subjects provided calls in both contexts; otherwise, we used a one-way ANOVA. We applied a sequential Bonferroni correction ($\alpha' = \alpha / (k - n + 1)$, where k is the number of tests, n is the number of significant tests; Bortz et al. 1990). Statistical analyses were calculated using the statistical package SPSS 8.0. All tests are two-tailed.

Selection of Calls in the Analyses

Differences between contact and alarm barks

We included in our analysis 100 alarm barks to lions, seven to cheetahs (*Acinonyx jubatus*), five to leopards, one to wild dogs, 46 to crocodiles, nine to pythons (*Python sebae*), eight to hippopotamuses (*Hippopotamus amphibius*), and one to a black mamba (*Dendroaspis polylepis*). We also recorded 21 barks given to an

unidentified stimulus. We were reasonably certain that these calls constituted alarm calls because the callers, a group of females sitting in a tree, all looked into the same direction and conspicuously peered into the distance. We included these calls to increase the number of individuals in the analysis. For the analysis of differences between contact and alarm barks, we limited the number of calls per female in each context to 20; thus, 12 calls given in response to a crocodile and five calls given in response to a snake were discarded. We aimed to sample calls from as many bouts as possible. However, in most of the cases we sampled more than one call from each bout. For females who provided more than 20 calls, we first sampled all calls recorded from that subject. We then randomly selected 20 calls from this pool. For females who provided less than 20 calls per context, we sampled all calls that were of sufficient quality. We therefore assume that any potential effect of order within a call bout was minimized.

In sum, we used 513 calls recorded from 24 females (181 alarm barks from 18 females with a median of 6.5 calls per female; and 332 contact barks from 22 females with a median of 18.5 calls per female; 16 females provided calls in both contexts). The number of calls per individual ranged from 1 to 20. Four of the acoustic parameters listed above (F_0 maximum, F_0 median, formant dispersion, and formant ratio) could not be determined for every call; there were only 393 of the 513 calls for which there were no missing values. Since we aimed to keep as many calls by as many different females in the analysis, we first performed a test run with these 393 calls. We found that the four parameters mentioned did not play a role in the discrimination of groups. We then reverted to the entire data set of 513 calls and excluded these four parameters from the analysis.

Interaction of call type and individuality

We examined individual call characteristics and the interaction of call type and individuality for five females who contributed a similar number calls to both contexts. Two of the females are sisters (CT and SS), and two are niece and aunt (LK and NI). Overall, we selected 186 calls for analysis; 18–20 of both alarm and contact barks per female, respectively, with the exception of CT for whom we only had 13 alarm barks. As mentioned before, a number of calls had missing values in four of the parameters (F_0 maximum, F_0 median, formant dispersion, and formant ratio). Thus, we first explored whether they played a role in discriminating among individuals. Since parameters characterizing the fundamental frequency (F_0) were important in distinguishing among individuals, we excluded all calls with this missing value; 179 calls remained in the analysis.

Differences in relation to predator class

In order to examine possible differences in the alarm bark given to different classes of predators, we performed a discriminant analysis on 100 alarm barks by 11 females given in response to lions (number of calls per female ranging between 1 and 20), and 46 alarm calls given by eight females in response to a crocodile (number of calls per female ranging between 1 and 16). In order to determine

whether either alarm call category was more or less similar to contact barks, we performed a discriminant analysis on the 46 crocodile alarm calls recorded from eight females, 46 randomly selected lion alarms recorded from 10 females, and 46 randomly selected contact calls recorded from 12 females.

Results

The Context of Alarm Barks

Most often, we were alerted to the presence of predators in the area by repeated calling of one or several individuals. In a typical encounter, one or several individuals would climb into a tree and call repeatedly as they monitored the predator's activity. The number of individuals calling and the behavior of other group members varied, apparently according to threat urgency. If the predator in question was several hundred meters away, only a few individuals typically gave alarm calls, while other group members continued to forage on the ground. If the predator had attacked or killed a group member, however, or if a potential predator suddenly appeared in the midst of the group, the entire group would flee and give alarm calls.

The presence of lions usually caused the most intense calling. Since 1992, we have observed one confirmed and several suspected predations by lions (see also Busse 1980). Often, after detecting lions, the baboons subsequently altered their direction of travel. Baboons also gave alarm calls in response to leopards, cheetahs, spotted hyena, and wild dogs. Leopards are a major source of predation in this population, especially at night (four confirmed and several suspected incidents). When baboons encountered a leopard during the day, they aggressively attacked it. We have witnessed over a dozen instances in which a large proportion of the group gathered around a leopard's lair and mobbed it while screaming and giving alarm calls. When the leopard attempted to escape, it was chased by individuals of all age/sex classes. We also observed baboons chasing cheetahs. The presence of wild dogs seldom caused much overt anti-predator behavior.

Another serious source of danger are crocodiles. We have observed three instances when crocodiles attacked baboons as they were drinking from the river or a large water hole. The alarm calls we were able to record, however, were given by females foraging in trees at the edge of the river where a crocodile was sunbathing. We also recorded calls given in response to hippopotamuses swimming by with only small parts of their heads visible above the water's surface. We assume that the callers mistook these stimuli for crocodiles, but nonetheless kept these calls in a separate category. Baboons were never observed to give alarm calls in response to raptors. During the course of the study, members of this particular group also gave no alarm calls to human observers.

Both contact and alarm barks are loud and can be heard from at least 200 m away, as estimated by the distance we walked from hearing the animals until we located them in the field. The sound pressure level for contact barks averages 69 dB (range: 65–71 dB) at 8–12 m, based on the mean values from five females. Although we have no SPL readings for alarm barks, it is our impression that both

call types have a similar amplitude. Contact and alarm barks differ in their frequency of occurrence. In 1998, we noted a mean (\pm SD) call rate of 0.69 ± 2.2 calls/h for alarm barks and 4.5 ± 9.1 calls/h for contact barks. In the 15-day observation period in 1999, we recorded a mean call rate for contact barks of 7.3 ± 9.5 calls/h, but no alarm barks.

The mean (\pm SD) call interval was 18 ± 7 s for alarm barks and 22 ± 7 s for contact barks, with a minimum interval across individuals of 7.2 ± 6.4 s for alarm calls (range 1–17 s), and 8.1 ± 6.2 s (range 1–19 s) for contact barks. For those eight females that provided interval readings for both categories, a pair-wise comparison yielded no significant differences for either mean or minimum interval (exact Wilcoxon signed-ranks test: mean interval $n = 8$, $T + = 19$, ns; minimum interval $T + = 6$, 2 ties, ns).

Acoustic Characteristics of Alarm and Contact Barks

Fig. 1 shows spectrograms of the barks given by one female in two different contexts: when separated from the group and when she had detected a crocodile. The spectrograms show that these calls grade from a tonal into a harsh variant and that there are intermediate forms between the two extremes. As a first test of the hypothesis that alarm and contact barks are acoustically different, we conducted a discriminant function analysis with 'context' as the grouping variable. The average correct assignment was 86.7%; a 10-fold cross validation yielded an average correct assignment of 82.2%.

There were 12 parameters with a within-group pooled correlation with the discriminant function > 0.2 . We performed pair-wise univariate comparisons of these parameters for those 16 females that provided calls in both contexts. Table 1 lists the statistics for those variables that showed the highest correlation with the discriminant function. In general, alarm barks are significantly shorter, higher-



Fig. 1: Spectrograms of one adult female's barks given when she had lost contact to the troop (four calls to the left) and when she had detected a predator (four calls to the right). Spectrograms depict both typical variants of the respective context category (tonal vs. harsh bark), but also show that intermediate variants may occur in both contexts

Table 1: Acoustic parameters that vary significantly between contexts. Mean and SD from 16 females that provided calls in both contexts with results from pair-wise comparison between contexts (Wilcoxon matched-pairs signed-rank test, $n = 16$), and pooled within-groups correlation with discriminant function

Parameter	Alarm barks		Contact barks		z	p	Correlation
	Mean	SD	Mean	SD			
Duration [ms]	194	46	291	42	-3.516	**	0.623
DFA start [Hz]	774	92	569	70	-3.464	**	-0.491
Noise [%]	62	21	38	15	-2.947	*	-0.356
PF jump [Hz]	289	107	461	122	-2.999	*	0.334
DFB local modulation	48	7	57	6	-3.361	**	0.281
PF max location	0.43	0.08	0.37	0.04	-2.741	*	-0.274
PF max modulation	133	47	211	63	-2.999	*	0.273
FLS1 mean peak [Hz]	901	76	792	90	-3.154	*	-0.258
PF start [Hz]	854	106	652	113	-3.464	**	-0.254
DFB1 trend	-0.08	0.36	-0.07	0.07	-0.983	ns	-0.248
FLS1 mean range [Hz]	1044	230	906	213	-1.655	ns	-0.231
DFB max [Hz]	760	144	652	80	-2.637	*	-0.20

* $p \leq 0.017$, ** $p \leq 0.001$.

pitched, and noisier than contact barks. It appears that non-linear effects also play a role in the production of barks, as some of the calls exhibit period-doubling, phase shifts, and biphonation (e.g. the contact bark of LK depicted in Fig. 4), all features diagnostic of non-linear effects on phonation. However, an inspection of spectrograms suggested that these features did not map systematically onto the classification of calls in the analysis.

Fig. 2 presents the frequency distribution of the discriminant coefficients. The figure depicts a bimodal distribution of coefficients with an overlapping region. Calls represented at either end of the distribution are most different from each other; they are associated with a high assignment probability to their respective context category. Typical exemplars of both context categories are represented in the respective peaks of this bimodal distribution. Calls in the overlapping region exhibit a low assignment probability. Contact barks with a discriminant score of -0.5 or smaller were assigned to the category ‘alarm barks’, and vice versa.

Individual Differences

We first checked whether the differences in the acoustic structure of barks were due simply to individual variation in call characteristics. However, with the exception of one individual (SS), the percentage of cases that were misclassified in the analysis was distributed relatively evenly among subjects: 16 of the 24 females provided calls that were classified incorrectly. Fig. 3 presents the individual distributions of four of the females in the analysis. For each female, there was a

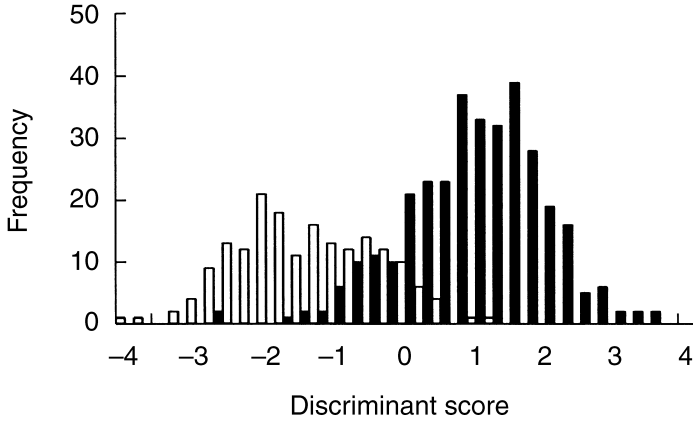


Fig. 2: Distribution of discriminant scores. Open bars: alarm barks; black bars: contact barks. Calls represented at the tail ends of the distribution differ most and can be easily assigned to their actual category. Calls in the overlapping region are indistinguishable to the analysis and have a low assignment probability to their actual category

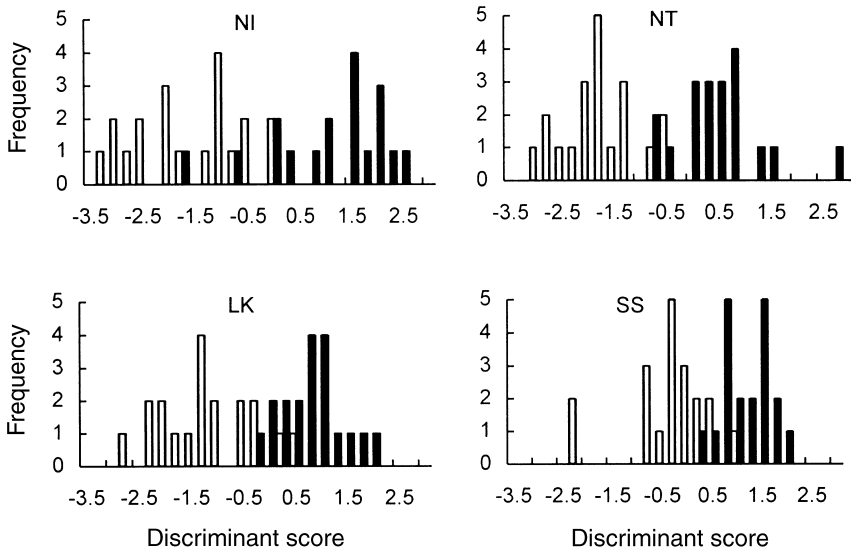


Fig. 3: Distributions of discriminant scores for four females. Open bars: alarm barks; black bars: contact barks. The four distributions show that the finding made for the entire set of calls across all callers also holds at an individual level

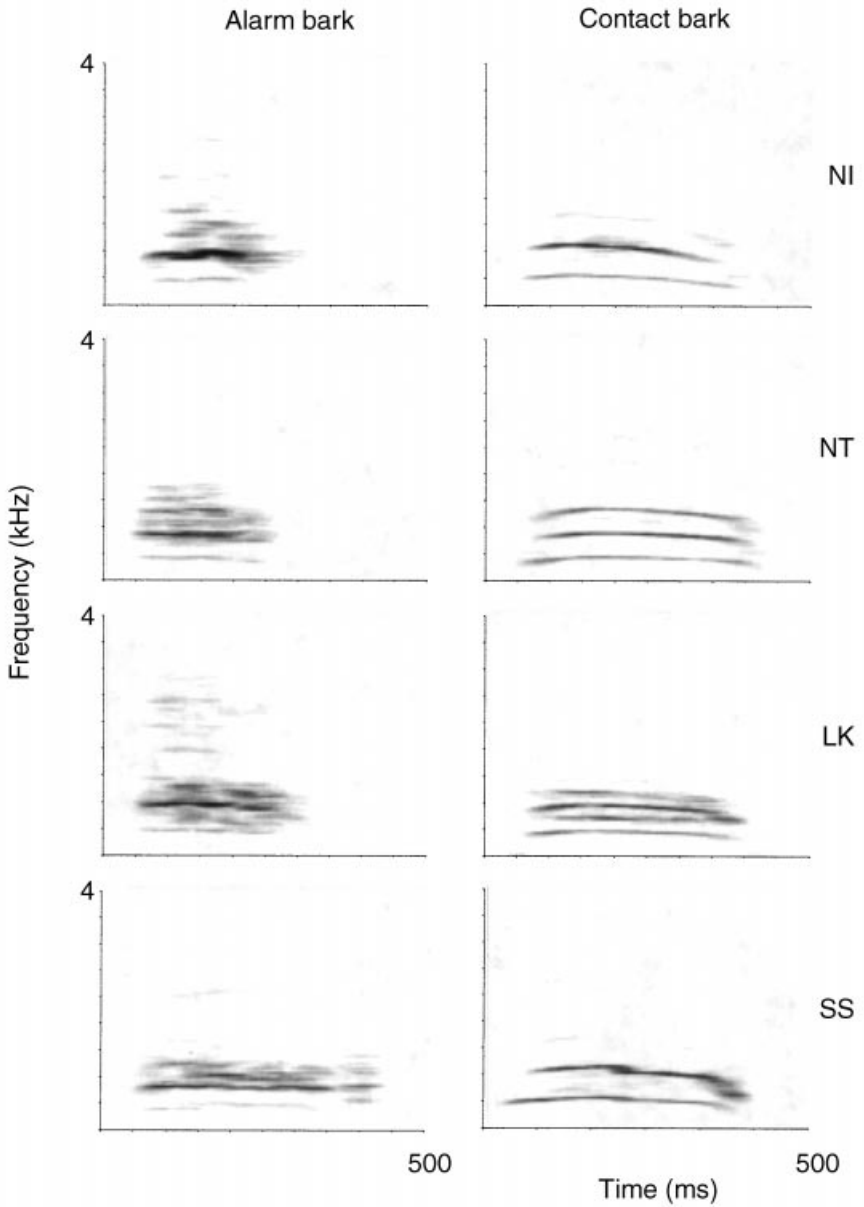


Fig. 4: Spectrograms of calls of the same four females whose individual distribution of discriminant coefficients is presented in Fig. 3. According to the outcome of the discriminant function analysis, these calls represent typical exemplars of their respective context categories

relatively even distribution of calls along the discriminant function. Female SS's calls also showed a bimodal distribution, but relative to the group distribution, her calls were shifted towards a more contact bark-like structure. This was due mainly to the fact that her calls were generally of longer duration than any other female's. Fig. 4 shows spectrograms of calls from the same four females. These calls had a high assignment probability to their respective context category; that is, they were represented in the tail end of the distribution of discriminant coefficients. The spectrograms illustrate that, despite appreciable individual variation, the same acoustic characteristics distinguished different individuals' alarm and contact barks.

When we examined differences between individuals across contexts, the average correct assignment to individual was 86.9% ('leave-one-out' validation: 69.3%). The analysis established four discriminant functions. The parameters with the highest correlation with these functions are listed in Table 2. We then performed the discriminant function analysis separately for each context category, to check whether parameters decisive for discriminating individuals remained the same across different call categories. The average correct assignment for the five females was 98.9% ('leave-one-out' validation: 71.4%) for alarm barks and 100% ('leave-one-out' validation: 60%) for contact barks. Table 2 also provides the parameters most suitable for discriminating among individuals within context categories.

Fig. 5 shows the individual distributions for the two parameters, call duration and the mean central frequency. For alarm barks, call duration is especially useful in discriminating female SS from all the other four females in the analysis. However, call duration also varies significantly between four other pairs of females (one-way ANOVA with Bonferroni corrected post hoc comparison, $p < 0.05$). For contact barks, call duration differs significantly only between SS and all other females. For the distribution of the mean central frequency, in contrast, there is no such correspondence between individual values across the two call types. Although some acoustic characteristics transferred across call types, others did not. Conse-

Table 2: Parameters that showed the highest correlation with the discriminant functions established to discriminate among individuals when alarm and contact barks were combined or when they were analyzed separately

Call Category	Discriminant function			
	Function 1	Function 2	Function 3	Function 4
Alarm and contact barks	Call duration FLS1 range	PF trend DFB max mod	Range mean DFB number	PF max DFA1 max
Alarm barks only	Call duration Consistency	Central frequency DFA1 start	F lw max range PF start	F0 max only FLS2%
Contact barks only	Range mean DFB number	Central frequency DFB2 mean	PF trend Call duration	DF1 local mod FLS2%

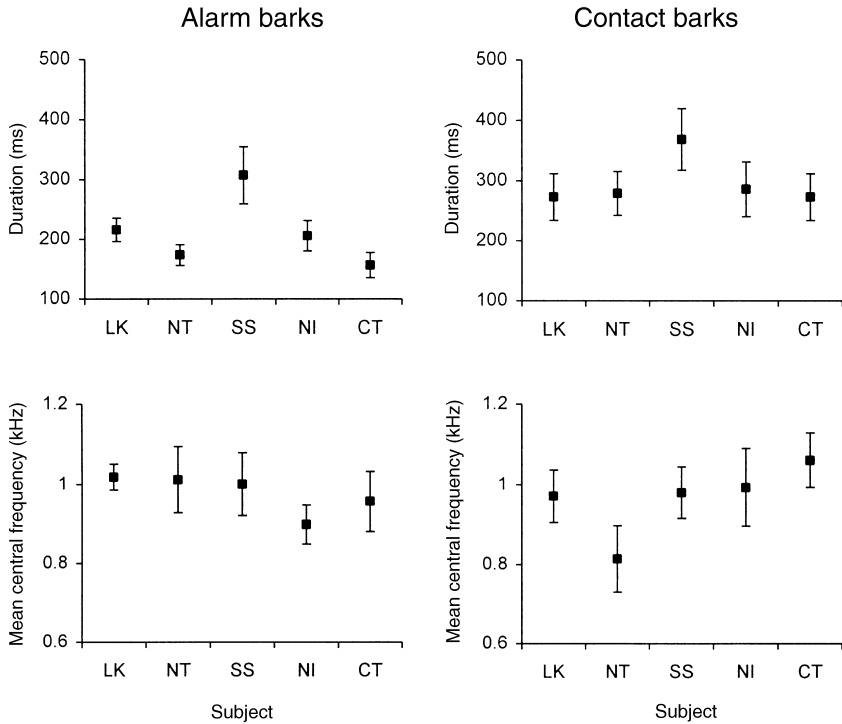


Fig. 5: Distribution of two acoustic parameters, call duration and central frequency, between contexts and among individuals. Whereas call duration shows the same relative distribution in both contexts, the distribution of the central frequency among individuals differs significantly between contexts

quently, it was difficult to predict individual identity in one call type from knowledge of the characteristics in the other.

Differences in the Alarm Barks Given to Different Predator Types

When we examined the calls for differences in relation to different classes of predators, we obtained an average correct assignment of 84.9% (cross-validated set: 70.4%). The most decisive parameters for discriminating between calls given to lions and calls given to crocodiles were all related to the first dominant frequency band: local modulation ($F = 14.6$; $p \leq 0.001$), maximum frequency ($F = 11.6$; $p < 0.01$), and global modulation ($F = 12.9$; $p < 0.01$; one-way ANOVA on individual means with $n = 19$, $df = 1, 17$). Calls given in response to crocodiles were more strongly modulated and the peak of the first dominant band was higher.

We next examined whether either alarm call category was more or less similar to contact barks. Fig. 6 shows a plot of the discriminant scores for the three

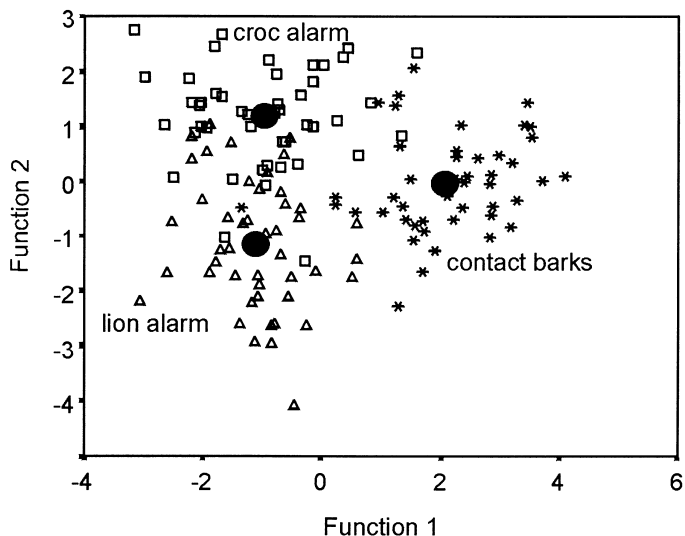


Fig. 6: Distribution of the discriminant scores for lion alarms (Δ), crocodile alarms (\square), and contact barks ($*$; $n = 46$ for each category) along the two canonical discriminant functions established to discriminate among the three categories. Group centroids are represented by black circles. The plot illustrates that alarm barks given in response to lions as opposed to crocodiles are different from each other and both different from contact barks

groups. The first discriminant function separates the contact calls from the two alarm call categories, and the second function separates the alarm call categories. Parameters that correlate with the first discriminant function are call duration, distribution of the frequency amplitude (first quartile) at start, and peak frequency at start. Parameters that correlate with the second function are the maximum modulation of the 1st dominant frequency band, the maximum frequency of the 1st dominant frequency band, and the global modulation of the 1st dominant frequency band, replicating the findings of the previous analyses. The group centroids of both alarm call categories are equidistant from the group centroid of the contact calls. That is, although there are significant differences between the alarm barks given in response to lions as opposed to crocodiles, these calls vary along a different dimension to that of alarm and contact barks. In other words, they are different from each other, and both are different from contact barks.

The sample sizes for alarm calls given in response to cheetahs, wild dogs, hippos, and especially snakes and leopards were too small to perform an analysis that controlled for individual differences in the calling. We therefore did not attempt an analysis of these calls. However, compared to contact barks, their acoustic characteristics fell well within the range of alarm barks.

Discussion

The barks of female baboons vary along a number of different acoustic dimensions. The acoustic parameters that characterize contact barks are significantly different from those that characterize alarm barks. However, there are also intermediate variants that fall in between prototypical cases of either call type. The occurrence of such intermediate variants is not due simply to a smearing of distinct characteristics across a large number of individuals, but can be replicated within individuals. Within the alarm bark category, there are slight but significant differences between calls given in response to lions and those given in response to crocodiles. Again, however, each alarm bark type shows intermediate variants that resemble the other type. Finally, there are consistent, significant differences among different individuals' calls. As a result, the calls potentially provide rich information to the recipients of these signals.

Individual differences in calls have been shown for a variety of species, and a number of playback studies have shown that these differences are perceptually salient (Rendall et al. 1996; Owren et al. 1997; Cheney & Seyfarth 1997; Hammerschmidt & Fischer 1998a). Using linear prediction coefficient (LPC) analysis, Rendall et al. (1998) suggested that individuality is predominantly caused by differences in the filter function of the vocal tract. In this study, individual differences were present, but could not be documented in the parameters derived from LPC analysis. This might be due to the fact that we used a lower number of coefficients than in Rendall et al.'s study. Nonetheless, our results suggests that individuality can be expressed through a wider variety of acoustic features than those solely related to the filter characteristics of the vocal tract (see also Hammerschmidt & Todt 1995).

An inspection of spectrograms showed that some barks exhibited intermittent sub-harmonics, the appearance of a second independent frequency ('biphonation'), or sudden transitions from linear to chaotic dynamics. Such phenomena indicate underlying non-linear dynamic effects in sound production (Wilden et al. 1998). The general phenomena that characterize non-linear systems (periodic doubling/halving, and chaotic oscillation) are also well known in human vocalizations (Herzel et al. 1995). The communicative significance of these phenomena, however, remains unclear. As a result, in the analysis reported here, we retained the phenomenological approach to delineate call characteristics. A previous study on Barbary macaques suggests that results obtained with this method appear to correspond well with the animals' own classification of calls (Fischer 1998). In the future, it will be important to extend our understanding of the mechanisms underlying vocal production in order to link acoustic features more clearly to physiological measures (see Fitch & Hauser 1995; Fitch & Giedd 1999).

The fact that contact and alarm barks are acoustically graded and sound alike is puzzling from a functional perspective. Theory suggests that calls serving markedly different functions should show marked acoustic differences, especially when they are broadcast over large distances (Marler 1965, 1967). According to this hypothesis, alarm barks should be unambiguously distinct from contact barks.

Vervet alarm calls, for example, are not only acoustically distinct from each other, but also form such vocalizations as inter-group calls (Cheney & Seyfarth 1988, 1990).

One possible explanation is that the barks of female baboons express the same general affective state. Within this general affective state, however, group separation and predator encounters evoke slightly different forms of excitement or fear, which are related to the acoustic variation between contact and alarm barks. The variation in acoustic structure between contact and alarm barks complies with the predictions of Morton's emotional-structural rules: alarm calls, presumably being linked to a higher arousal, are generally shorter, noisier, and higher-pitched (Morton 1977). However, this view begs the question of why two very different contexts should evoke similar sorts of affective states, particularly when, in other species – for example Barbary macaques (Hammerschmidt & Fischer 1998b) – those same contexts have resulted in the evolution of different calls.

Models stressing the emotional component in animal signals have largely ignored the cognitive processes underlying the caller's assessment of a given situation. Along with expressing emotion, the baboons' alarm and contact barks may also be viewed as reflecting the caller's mental representation of specific events in the external world (Cheney & Seyfarth 1990). It is to be hoped that future research will help to unveil the interplay between cognitive and motivational components on vocal production. Of specific interest is the question of whether these factors act independently on vocal production or whether cognitive processes trigger distinct emotional states that are linked to vocal production. Certainly, the results of playback experiments on several species are consistent with the view that calls evoke mental representations of specific events in listeners, who respond accordingly (Seyfarth et al. 1980).

Despite encountering high levels of predation, chacma baboons apparently use a call system that allows some slack or ambiguity in the acoustic structure of vocalizations. Baboons' responses appear to depend not just on signal content, but also on context and other cues in their environment. This suggestion supports the results of Rendall et al. (1999), who showed that call structure, the context in which the call was presented, and caller identity all influenced baboons' responses to different grunt types. It seems possible that the barks of female baboons constitute a more ancestral form of call system that has not been subjected to as much selection pressure as the vervet's alarm calls. The supposition that both context and acoustic structure influence receivers' responses may also help to explain why baboons' lion and crocodile alarm barks are only slightly different acoustically, even though the two classes of predators – and the escape responses they require – are markedly different. Perhaps the presence of both aerial and ground predators, which often require qualitatively different escape responses, plays a crucial role for establishing structurally distinct alarm calls. This view is supported by the finding that such distinct alarm calls have evolved independently in birds, squirrels, and primates (Marler 1977b; Klump & Shalter 1984).

Theories concerned with the evolution of referential signals often use the vervet monkey's relatively discrete alarm calls as a model (Marler 1977a, b; Cheney &

Seyfarth 1990). It seems increasingly likely, however, that vervets and other members of the genus *Cercopithecus* may be atypical among non-human primates in possessing such discrete vocalizations (Struhsaker 1967; Marler 1973; Seyfarth et al. 1980; Zuberbühler et al. 1999). The fact that vervets, which live in relatively open habitats, have a rather discrete repertoire, and the observation that baboons' long distance calls are acoustically graded, challenge the hypothesis that there is a simple relationship between the morphology of a species' vocal repertoire and its physical and social environment. It is noteworthy that the vocal repertoires of chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) are acoustically graded (Marler 1976; Seyfarth et al. 1994; Mitani et al. 1996). There is as yet no evidence that any of the great apes' calls serve a referential function – at least not in the ways that many vervet monkey calls do. Baboons, along with many other species possessing relatively graded vocal repertoires (e.g. macaques), may therefore provide a better model for the evolution of human speech than do vervets. At the very least, baboon vocalizations provide intriguing comparative data that may force us to rethink previous hypotheses about signal design and evolution.

Acknowledgements

We thank the Office of the President and the Department of Wildlife and National Parks of the Republic of Botswana for permission to conduct research in the Moremi Wildlife Reserve. Mokupi Mokupi helped with the data collection. JF is grateful to Markus Metz for his support and company in the field. Our thanks go to the Longden family for friendship and hospitality at Borobonche. We would also like to thank to everybody at Ensign Agencies, Mack Air, and Gametrackers Botswana for logistical support. Drew Rendall and two anonymous reviewers helped to improve the manuscript. This research was supported by the DFG (Fi 707/2–1) and KFN (JF), and by NSF grant IBN 9514001, NIH grant HD-29483, the National Geographic Society, the Research Foundation and the Institute for Research in Cognitive Science of the University of Pennsylvania (DLC and RMS).

Literature Cited

- Beeman, K. 1996: SIGNAL Operation Manual. Engineering Design, Belmont.
- Bortz, J. 1993: Statistik für Sozialwissenschaftler. Springer, Berlin.
- Bortz, J., Lienert, G. A. & Boehnke, K. 1990: Verteilungsfreie Methoden in der Biostatistik. Springer, Berlin.
- Bulger, J. B. 1993: Dominance rank and access to estrous females in male savanna baboons. *Behaviour* **124**, 89–122.
- Bulger, J. B. & Hamilton, W. J. 1988: Inbreeding and reproductive success in a natural chacma baboon (*Papio ursinus*) population. *Anim. Behav.* **36**, 574–578.
- Busse, C. 1980: Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Bot. Notes. Rec.* **12**, 15–21.
- Byrne, R. W. 1981: Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. *Behaviour* **78**, 283–313.
- Cheney, D. L. & Seyfarth, R. M. 1988: Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim. Behav.* **36**, 477–486.
- Cheney, D. L. & Seyfarth, R. M. 1990: How Monkeys See the World. Univ. of Chicago Press, Chicago.
- Cheney, D. L. & Seyfarth, R. M. 1997: Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Anim. Behav.* **54**, 409–418.
- Cheney, D. L. & Seyfarth, R. M. 1999: Recognition of other individuals' social relationships by female baboons. *Anim. Behav.* **58**, 67–75.

- Cheney, D. L., Seyfarth, R. M. & Palombit, R. 1996: The function and mechanisms underlying baboon 'contact' barks. *Anim. Behav.* **52**, 507—518.
- Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995: The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Anim. Behav.* **50**, 249—257.
- Darwin, C. 1872: *The Expression of the Emotions in Man and Animals*. Murray, London.
- Fischer, J. 1998: Barbary macaques categorize shrill barks into two call types. *Anim. Behav.* **55**, 799—807.
- Fischer, J., Hammerschmidt, K. & Todt, D. 1995: Factors affecting acoustic variation in Barbary-macaque (*Macaca sylvanus*) disturbance calls. *Ethology* **101**, 51—66.
- Fitch, W. T. & Giedd, J. 1999: Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *J. Acoust. Soc. Am.* **106**, 1511—1522.
- Fitch, W. T. & Hauser, M. D. 1995: Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on 'honest' advertisement. *Am. J. Primatol.* **37**, 191—219.
- Fitch, W. T. & Hauser, M. D. 2000: Unpacking 'honesty': vertebrate vocal production and the evolution of acoustic signals. In: *Acoustic Communication* (Simmons, A. M., Fay, R. & Popper, A. N., eds). Springer Verlag, New York.
- Hall, K. R. L. & DeVore, I. 1965: Baboon social behavior. In: *Primate Behavior: Field Studies of Monkeys and Apes* (DeVore, I., ed.). Holt, Rinehart and Winston, New York, pp. 53—110.
- Hamilton, W. J. & Bulger, J. B. 1990: Natal male baboon rank rises and successful challenges to resident alpha males. *Behav. Ecol. Sociobiol.* **26**, 357—362.
- Hamilton, W. J., Buskirk, R. E. & Buskirk, W. H. 1976: Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. *Ecology* **57**, 1264—1272.
- Hammerschmidt, K. 1990: Individuelle Lautmuster bei Berberaffen (*Macaca sylvanus*): Ein Ansatz zum Verständnis ihrer vokalen Kommunikation. PhD thesis, FU Berlin, Berlin.
- Hammerschmidt, K. & Fischer, J. 1998a: Maternal discrimination of offspring vocalizations in Barbary macaques (*Macaca sylvanus*). *Primates* **39**, 231—236.
- Hammerschmidt, K. & Fischer, J. 1998b: The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology* **104**, 203—216.
- Hammerschmidt, K. & Todt, D. 1995: Individual differences in vocalizations of young Barbary macaques (*Macaca sylvanus*): A multi-parametric analysis to identify critical cues in acoustic signalling. *Behaviour* **132**, 381—399.
- Herzel, H. P., Berry, D., Titze, I. & Steinecke, I. 1995: Nonlinear dynamics of the voice: signal analysis and biomechanical modeling. *Chaos* **5**, 30—34.
- Klump, G. M. & Shalter, M. D. 1984: Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. *Z. Tierpsychol.* **66**, 189—226.
- Leger, D. W., Owings, D. H. & Boal, L. M. 1979: Contextual information and differential responses to alarm whistles in California Ground squirrels. *Z. Tierpsychol.* **49**, 142—155.
- Macedonia, J. M. 1990: What is communicated in the antipredator calls of Lemurs: evidence from playback experiments with Ringtailed and Ruffed Lemurs. *Ethology* **86**, 177—190.
- Macedonia, J. M. & Evans, C. S. 1993: Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology* **93**, 177—197.
- Marler, P. 1965: Communication in monkeys and apes. In: *Primate Behavior: Field Studies of Monkeys and Apes* (DeVore, I., ed.). Holt, Rinehart and Winston, New York, pp. 544—584.
- Marler, P. 1967: Animal communication signals. *Science* **157**, 769—774.
- Marler, P. 1973: A comparison of the vocalizations of red-tailed monkeys and bluemonkeys: *Cerco-pithecus ascanius* and *C. mitis* in Uganda. *Z. Tierpsychol.* **33**, 223—247.
- Marler, P. 1976: Social organization, communication and graded signals: the Chimpanzee and the Gorilla. In: *Growing Points in Ethology* (Bateson, P. P. G. & Hinde, R. A., eds). Cambridge Univ. Press, Cambridge UK, pp. 239—280.
- Marler, P. 1977a: Primate vocalizations: affective or symbolic?. In: *Progress in Ape Research* (Bourne, G. H., ed.). Academic Press, New York, pp. 85—96.
- Marler, P. 1977b: The structure of animal communication sounds. In: *Recognition of Complex Acoustic Signals* (Bullock, T. H., ed.). Springer Verlag, Berlin, pp. 17—35.

- Marler, P. 1992: Functions of arousal and emotion in primate communication: a semiotic approach. In: *Topics in Primatology*, Vol. 1: Human Origins (Nishida, T., McGrew, W. S., Marler, P., Pickford, M. & De Waal, F. B. M., eds). Univ. of Tokyo Press, Tokyo, pp. 225–233.
- Mitani, J. C., GrosLouis, J. & Macedonia, J. M. 1996: Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *Int. J. Primatol.* **17**, 569–583.
- Morton, E. S. 1977: On the occurrence and significance of motivation–structural rules in some bird and mammal sounds. *Am. Nat.* **111**, 855–869.
- Owings, D. H. & Morton, E. S. 1998: *Animal Vocal Communication: A New Approach*. Cambridge Univ. Press, Cambridge.
- Owings, D. H. & Virginia, R. A. 1978: Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z. Tierpsychol.* **46**, 58–70.
- Owren, M. J. & Bernacki, R. H. 1988: The acoustic features of vervet monkey alarm calls. *J. Acoust. Soc. Am.* **83**, 1927–1935.
- Owren, M. J. & Linker, C. 1995: Some analysis methods that may be useful to acoustic primatologists. In: *Current Topics in Primate Vocal Communication* (Zimmermann, E., Newman, J. D. & Jürgens, U., eds). Plenum Press, New York, pp. 1–28.
- Owren, M. J., Seyfarth, R. M. & Cheney, D. L. 1997: The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for production processes and functions. *J. Acoust. Soc. Am.* **101**, 2951–2963.
- Palombit, R. A., Seyfarth, R. M. & Cheney, D. L. 1997: The adaptive value of ‘friendships’ to female baboons: experimental and observational evidence. *Anim. Behav.* **54**, 599–614.
- Pimentel, R. A. & Frey, D. F. 1978: Multivariate analysis of variance and discriminant analysis. In: *Quantitative Ethology* (Colgan, P. W., ed.). Wiley, New York, pp. 247–274.
- Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2000: Proximate factors mediating ‘contact’ calls in adult female baboons and their infants. *J. Comp. Psychol.* **114**, 36–46.
- Rendall, D., Owren, M. J. & Rodman, P. S. 1998: The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *J. Acoust. Soc. Am.* **103**, 602–614.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1996: Vocal recognition of individuals and kin in free ranging rhesus monkeys. *Anim. Behav.* **51**, 1007–1015.
- Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999: The meaning and function of grunt variants in baboons. *Anim. Behav.* **57**, 583–592.
- Ross, K. 1987: *Okavango: Jewel of the Kalahari*. Macmillan, New York.
- Schrader, L. & Hammerschmidt, K. 1997: Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach. *Bioacoustics* **7**, 274–265.
- Seyfarth, R. M. & Cheney, D. L. 1997: Behavioral mechanisms underlying vocal communication in nonhuman primates. *Anim. Learn. Behav.* **25**, 249–267.
- Seyfarth, R. M., Cheney, D. L., Harcourt, A. H. & Stewart, K. J. 1994: The acoustic features of Gorilla double grunts and their relation to behaviour. *Am. J. Primatol.* **33**, 31–50.
- Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980: Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science* **210**, 801–803.
- Silk, J. B., Seyfarth, R. M. & Cheney, D. L. 1999: The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour* **136**, 679–703.
- Struhsaker, T. T. 1967: Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: *Social Communication Among Primates* (Altmann, S. A., ed.). Univ. of Chicago Press, Chicago.
- Wilden, I., Herzel, H., Peters, G. & Tembrock, G. 1998: Subharmonics, biphonation, and deterministic chaos in mammal vocalizations. *Bioacoustics* **9**, 171–197.
- Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999: Conceptual semantics in a nonhuman primate. *J. Comp. Psychol.* **113**, 33–42.

Received: February 21, 2000

Initial acceptance: June 2, 2000

Final acceptance: July 7, 2000 (R. Noë)

Appendix: Acoustic Parameters Used in the Analysis

Parameter	Description
Fo max [Hz]	Maximum value fundamental frequency
FO median [Hz]	Median value fundamental frequency across all time segments
DFA1 start [Hz]	Frequency at which the distribution of frequency amplitudes reaches 1st quartile at the beginning of the call
DFA1 mean [Hz]	Mean across time segments
DFA1 max [Hz]	Maximum value in all time segments
DFA2 mean [Hz]	Frequency at which the amplitude distribution reaches the second quartile, mean across time segments
DFB1 start [Hz]	DFB1 at the beginning of the call
DFB1 max [Hz]	Maximum value in all time segments
DFB1 mean [Hz]	Mean across all time segments
DFB1 local modulation	Number of times the original curve crosses the average
DFB1 max modul. [Hz]	Max difference between original DFB and average
DFB1 slope [Hz/s]	Slope of the trend (i.e. the linear regression determined by least squares method)
DFB trend difference [Hz]	Maximum difference between regression function and actual value of the DFB
DFB2 mean [Hz]	Mean across all time segments for 2nd dominant frequency band
DFB3%	Percentage of time segments with a third dominant frequency band
DFB start difference [Hz]	Difference between 1st and 2nd dominant frequency band at start
DFB mean difference [Hz]	Mean difference between 1st and 2nd dominant frequency band
DFB number	Mean number of dominant frequency bands detected in call
DFB ratio	Amplitude ratio between DFB1 and DFB2 (DFB1/DFB2)
FLS1 max range [Hz]	Maximum frequency range of 1st FLS
FLS1 mean range [Hz]	Mean frequency range of 1st FLS
FLS1 max peak [Hz]	Highest peak of the 1st FLS
FLS1 mean peak [Hz]	Mean value of peaks of the 1st FLS across all time segments
FLS2%	Percentage of time segments in which a second FLS could be detected
Range max [Hz]	Maximum difference between highest and lowest frequency
Range mean [Hz]	Mean difference between highest and lowest frequency across all time segments
PF start [Hz]	Frequency with the highest amplitude at start of call
PF mean [Hz]	Mean of the frequencies with the highest amplitude across all time segments
PF max [Hz]	Frequency of the maximum amplitude of a call
PF max location	Relative position of maximum in the call; ranges between 0 and 1
PF modulation	Number of times the original curve crosses the average

Parameter	Description
PF max modulation [Hz]	Max difference between the actual value of the PF and the average
PF jump [Hz]	Max difference of the PF in two consecutive time segments
PF slope	Slope of the trend (regression line) of the PF values of the time segment
noise [%]	Percentage of time segments in which no harmonic structure could be detected
complex [%]	Percentage of time segments with a complex structure
Max jump location	Relative location of the max difference of the PF between two adjacent time segments
duration [ms]	Time from onset to end of call
Formant 1 [Hz]	Frequency of the peak of the first formant
Formant dispersion [Hz]	Difference between F1 and F2
Formant ratio	Amplitude ratio between F1 and F2 (F1/F2)