Acoustic features of male baboon loud calls: Influences of context, age, and individuality

Julia Fischer[a]
Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, Pennsylvania 19104

Kurt Hammerschmidt
German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany

Dorothy L. Cheney
Department of Biology, University of Pennsylvania, Leidy Building, 415 South University Avenue, Philadelphia, Pennsylvania 19104

Robert M. Seyfarth
Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, Pennsylvania 19104

The acoustic structure of loud calls ("wahoos") recorded from free-ranging male baboons (*Papio cynocephalus ursinus*) in the Moremi Game Reserve, Botswana, was examined for differences between and within contexts, using calls given in response to predators (alarm wahoos), during male contests (contest wahoos), and when a male had become separated from the group (contact wahoos). Calls were recorded from adolescent, subadult, and adult males. In addition, male alarm calls were compared with those recorded from females. Despite their superficial acoustic similarity, the analysis revealed a number of significant differences between alarm, contest, and contact wahoos. Contest wahoos are given at a much higher rate, exhibit lower frequency characteristics, have a longer "hoo" duration, and a relatively louder "hoo" portion than alarm wahoos. Contact wahoos are acoustically similar to contest wahoos, but are given at a much lower rate. Both alarm and contest wahoos also exhibit significant differences among individuals. Some of the acoustic features that vary in relation to age and sex presumably reflect differences in body size, whereas others are possibly related to male stamina and endurance. The finding that calls serving markedly different functions constitute variants of the same general call type suggests that the vocal production in nonhuman primates is evolutionarily constrained. © *2002 Acoustical Society of America.* [DOI: 10.1121/1.1433807]

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I. INTRODUCTION

The loud, two-syllable barks given by adult male baboons (*Papio cynocephalus*) are familiar to anyone who has traveled through the wildlife reserves of Eastern or Southern Africa. These calls, or "wahoos" (Hall and DeVore, 1965), are louder than any other calls in the baboons' repertoire and appear to be adapted for long-range communication (Waser and Brown, 1984). Depending on wind conditions they are audible from more than one kilometer (Hall and DeVore, 1965). Wahoos typically consist of a loud bark—the "wa" syllable—and a second, lower amplitude, "hoo" syllable. Wahoos are given in three broadly different contexts: during predator encounters (alarm wahoos), during aggressive interactions with conspecifics (contest wahoos), and, less commonly, when a male has become separated from the group (contact wahoos). Alarm wahoos are given in response to a variety of different predators, including lions (*Panthera leo*), leopards (*P. pardus*), and crocodiles (*Crocodilus niloticus*). In some cases, the hoo syllable is hardly audible or drops out

entirely so that single wa syllables (barks) can also be heard. Contest wahoos appear to play a role in competitive interactions between males. They are frequently heard at dawn, when males commonly participate in a chorus of calling in apparent displays of dominance. They are also given during aggressive interactions, as males either chase each other or herd females (Buskirk *et al.*, 1974; Cheney and Seyfarth, 1977; Saayman, 1971). Males involved in such chases often engage in conspicuous arboreal displays. These chases appear to function at least in part as displays of stamina and fighting ability, and they usually involve higher-ranking males of adjacent ranks who appear to be challenging each other's dominance status. Finally, wahoos may also be given by males who appeared to have lost contact with the group. These calls appear to have the same function as the contact barks given by females, infants, and juveniles (Cheney *et al.*, 1996; Fischer *et al.*, 2001a; Rendall *et al.*, 2000).

In this paper, we present an analysis of the acoustic structure of wahoos given by male chacma baboons (*P.c. ursinus*). We first examine possible differences between contest and alarm wahoos. We then investigate the extent to which contest wahoos given in different contexts (e.g., male–male aggression versus herding of females) differ from one another. Next, we examine age differences within and

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[a]Current address: Julia Fischer, Max-Planck Institute for Evolutionary Anthropology, Inselstr. 22, 04103 Leipzig, Germany. Electronic mail: fischer@eva.mpg.de

between contexts. Finally, we focus on individual variation. Because the first syllable of the wahoo call, the wa, is similar to the single-syllable bark given by females (Fischer *et al.*, 2001a), and the two calls apparently develop from the same call type in juveniles (personal observation), we also explore differences in relation to sex. We examine age- and sex-related differences to test predictions about the relationship between body size and acoustic features.

A number of variables should provide cues to the body size of the caller. Specifically, the duration of loud calls such as wahoos should be related to lung capacity which in turn is related to body size (Fitch and Hauser, in press). Thus, we expect adult males to be able to produce longer calls than either younger males or females. Another acoustic parameter that is frequently related to body size is the fundamental frequency (Darwin, 1872; Morton, 1977; for a discussion see Fitch and Hauser, in press). We therefore predict that adult males will produce calls with a significantly lower fundamental frequency than either younger males or females. Cues to body size can also be provided by formant frequencies. The primary determinant of formant frequencies is the length of the vocal tract (Fant, 1960; Fitch, 1997; Liebermann and Blumstein, 1988). As Fitch (1997) demonstrated, a lengthening of the vocal tract tube leads to a decrease in the average spacing between successive formants ("formant dispersion"). If vocal tract length is correlated with body size, formant dispersion provides an honest cue to body size. In rhesus macaques (*Macaca mulatta*) and dogs (*Canis familiaris*), for instance, there is a close correlation between body size, vocal tract length, and formant dispersion (Fitch, 1997; Riede and Fitch, 1999). Accordingly, we expect a lower formant dispersion in adult males than in animals of other age or sex. By examining the relationship between call structure and function, we aim to formulate hypotheses about the potential information available to the receivers of these signals.

II. METHODS

A. Study site and subjects

The study site lies in the Moremi Wildlife Reserve in the Okavango Delta, Botswana, 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 over 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 group's home range in this 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. Matrilineal relatedness of all natal animals is known. A number of comprehensive studies describe aspects of the social behavior (Cheney *et al.*, 1996; Palombit *et al.*, 1999, 2000; Silk *et al.*, 1996, 1999), as well as the vocal communication of this population (Cheney *et al.*, 1996; Cheney and Seyfarth, 1997; Fischer *et al.*, 2000, 2001b; Rendall *et al.*, 1999, 2000). During the period of this study, group size ranged from 79 to 84 subjects.

B. 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 January 1998 and June 1999. Whenever a male within earshot started calling, we approached the subject and attempted to record his calls. 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. For the acoustic analysis, we used only calls given at a distance of 5–15 m from the microphone because estimates of some acoustic parameters can be influenced by signal transmission over large distances. This is particularly true for variables that characterize higher frequency components (K. Hammerschmidt and J. Fischer, unpublished data, 2001). Only calls whose context could be determined precisely were subjected to acoustic analysis.

C. Acoustic analysis

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 20 000 Hz using RTS (Engineering Design, Belmont, MA; Beeman, 1996) or COOL EDIT 96 (Syntrillium, Phoenix, AZ). To obtain a better frequency resolution, we first reduced the sample frequency to 10 000 Hz. 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: 5 ms; frequency range: 4000 Hz; frequency resolution: approximately 10 Hz). We sampled a mean of 2.9 calls per bout (median: 2, range: 1–13) from a total of 83 call bouts. In the contexts from which we sampled the calls, no high-amplitude vocalizations other than calls categorized as "wahoos" occurred. In some of the recording sessions, animals also uttered low-amplitude grunts which were not considered in the present analysis.

We submitted the resulting frequency time spectra to a custom software program (LMA 8.4) that extracts different sets of call parameters from acoustic signals (Hammerschmidt, 1990). Below, we briefly describe the underlying principle for the different groups of measurements. Figure 1 illustrates some of the variables considered in the analyses. First, we 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 that was noisy. Second, we measured the statistical distribution of the frequency amplitudes in the spectrum. For each time segment, the overall amplitude is determined. Subsequently, we calculated the frequency at which the distribution of the amplitude in the frequency spectrum (hereafter "distribution of frequency amplitudes") reaches the first and second quartile of the total distribution, respectively. Third, we calculated a set of parameters describing the first three dominant fre-
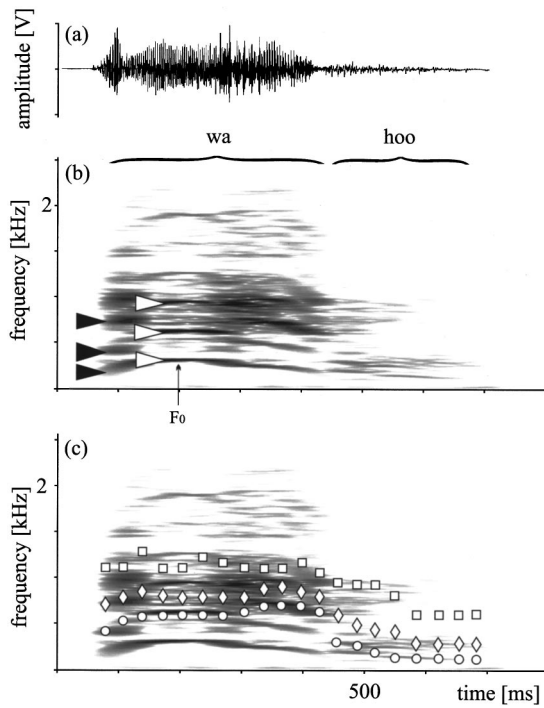
FIG. 1. (a) Amplitude and (b) spectrogram of a wahoo call indicating some of the variables determined in the acoustic analysis. Black triangles denote the first, second, and third dominant frequency at the beginning of the call; white triangles are in that given time segment. Depending on the call structure, the first dominant frequency may or may not correspond to the fundamental frequency. For this call segment, the fundamental corresponds to the first dominant frequency band. The two syllables are typically separated by a short interval of little energy, and hoo syllables consistently exhibit a much lower amplitude than wa syllables. (c) Distribution of frequency amplitudes in the spectrum. Circles mark the first dfa, diamonds the second dfa, and squares the third dfa for each time segment. Subsequently, the start and mean values for the first and second dfa were calculated.
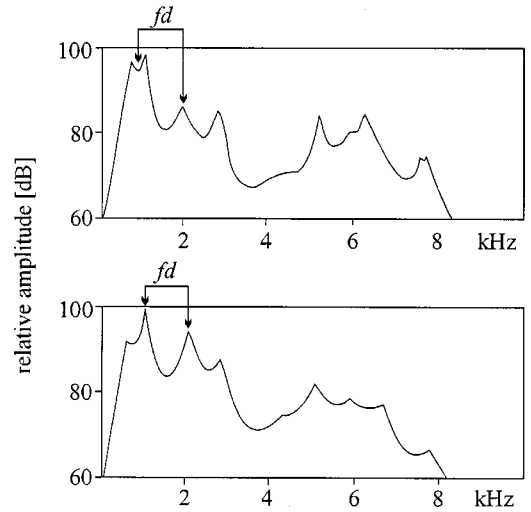

FIG. 2. Filter functions derived from an LPC analysis fitted with 23 coefficients. Both functions are derived from two contest wahoos given by the same individual. The upper graph has a lowest formant with a double peak, the lower graph with a single peak. Formant dispersion (fd) was calculated as the difference between the midpoint of the lowest two or the lowest peak, respectively, and the following peak.

quency 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 dominant frequency bands count from the lowest frequency up; the first dfb is not necessarily the dfb with the highest amplitude. Fourth, we determined the global energy distribution in the calls (''formant-like structures''). Fifth, we specified the location and the modulation of the peak frequency, the frequency with the highest amplitude in a certain time segment. Sixth, we determined the mean and maximum frequency range. We also calculated the duration of both the ''wa'' and the ''hoo'' syllable of the call and the ratio of the maximum amplitude of the wa versus the hoo syllable. Last, we used a cursor to measure the fundamental frequency in the middle third of the wa syllable (see the Appendix for a list of the calculated parameters). A description of the various algorithms is given in Schrader and Hammerschmidt (1997).

Because some calls exhibited diagnostics of period-doubling bifurcations (insertions of subharmonic episodes with approximately $F_0/2$, $3F_0/2$ etc.; see Wilden et al., 1998 for details), it appeared that nonlinear effects also play a role in the production of wahoos. We therefore inspected spectrograms visually and noted whether or not they exhibited signs of period doubling.

Additionally, we conducted a linear prediction coefficient (LPC) analysis using SOUNDSCOPE (GW Instruments, Somerville, MA) or SPEECHSTATION2 (Sensimetrics, Somerville, MA). LPC analysis is an alternative to Fourier analysis for describing the spectrum of a signal segment. We used two approaches. First, to obtain a more detailed analysis of the lower frequency range, we calculated 12 LPC coefficients from a 4096-pt FFT spectrum at a frequency range of 4000 Hz with SPEECHSTATION2. In this analysis, we determined the frequency of the peak of the first three formants (filtering frequency). Second, to obtain a higher resolution, we calculated 23 LPC coefficients from a 4096-pt FFT spectrum at a frequency range of 10 000 Hz with SOUNDSCOPE. For this analysis, we selected a 100-ms time segment of a tonal part of the wa syllable with a nearly constant fundamental frequency. To obtain a better characterization of the higher frequency parts, we used a pre-emphasis filter of 6 dB/octave, increasing the higher frequency components. From this analysis, we determined the location of the first eight peaks, the amplitude ratio between the peak i and peak i+1, and the difference between the frequency of peak i and peak i+1. It was not possible to analyze all of the hoo syllables in this way, as many either had a weak amplitude or were absent. This was particularly true for hoo syllables by adolescent and subadult males.

An inspection of the frequency distribution of the second formant revealed a bimodal distribution with a first peak around 1100 Hz and a second peak around 2000 Hz. This occurred because, in some cases, the peak detection algorithm identified two peaks in the function describing the lower vocal-tract resonances. For those cases that showed such a ''double peak,'' we determined the formant dispersion as the difference between the midpoint of the two lowest and the following peak (Fig. 2). Otherwise, we calculated the difference between the first and the second formant peak.

Finally, we examined call rate. First, we randomly se-

lected one bout per individual and measured the interval from the beginning of a call to the beginning of the subsequent call using COOLEDIT 96. A total of 22 bouts was chosen for analysis, recorded from a total of 16 subjects. On average, we measured 8.9 ± 6.2 ($\bar{x} \pm$ s.d.) intervals per bout. We then calculated the number of calls/min. To test for differences in call rate between the alarm and contest contexts, we applied the "repeated samples with missing values test" (Mundry, 1999), as not all subjects were represented in both contexts. This is a permutation test that delivers a variant of a Friedman one-way analysis of variance, providing a way to deal with missing values. We used 10 000 permutations. Due to the small sample size, we did not consider the call rate in the contact context for statistical analysis, and simply report the results below.

D. 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 characterizes 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. Discriminant function analysis has been successfully applied to determine acoustic differences between individuals or contexts in a number of studies (e.g., Fischer *et al.*, 2001a; Gouzoules and Gouzoules, 1989; Smith *et al.*, 1982).

Discriminant function analysis provides a classification procedure that assigns each call to its appropriate group (correct assignment) or to another group (incorrect assignment). For external validation, we used a tenfold cross validation in which we randomly selected roughly 90% of the data to calculate the discriminant functions and used the remaining 10% of cases for classification. We iterated this procedure ten times.

The percentage of calls classified correctly 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 (Bortz, 1993). This is particularly true for the "direct method," in which all variables are entered simultaneously. We preferred this method over the "stepwise procedure" because it preserves all available information. As a result, for those analyses with a smaller sample size we first explored the data set to identify variables that contributed to a discrimination of contexts or individuals and excluded those variables that did not vary among any of them. The amount of correct classification is also unaffected by nonindependent data points, in contrast to the significance test of the discriminant functions. We therefore only considered the classification results. For further statistical evaluation, we calculated the mean values per individual and context to avoid problems associated with pseudoreplication. In case where we used univariate statistics, we

TABLE I. Number of calls per individual male in the analyses of differences between alarm and contest contexts, and differences within the contest context. Callers marked with an asterisk were used in the analysis of individual differences.

Caller	Between contexts		Within contest context		
	Contest	alarm	Chase	Herd	Contest
AP*	20	6	4	20	6
AU*	18	6	13	11	2
DG		11			
EN*	19		2	14	4
KI	13			13	
KK*	17	9	8	10	20
RB	7	5		7	7
RY*	20		13		11
TH*	13	11	20	11	9
VE*	20		5	6	18
WA*	19	13	3	10	20
ZK	2			2	
Σ	168	61	68	104	90

applied a sequential Bonferroni correction ($\alpha' = \alpha/(k-n+1)$), where $k=$ number of tests, $n=$ number of significant tests). Statistical analyses were calculated using the statistical package SPSS 9.0. All tests are two-tailed. Unless otherwise stated, the significance level is set at $\alpha = 0.05$.

E. Data sets

The rationale for the selection of calls was to sample an even number of calls per individual and context from as many independent recordings as possible. We first entered all calls that we recorded into a database. Next, we pseudorandomly chose a given number of calls per recording session. In cases where an individual provided less than the required number of calls, all calls available were taken.

For acoustic analysis, we created different data sets. The first set was used to examine differences between contest and alarm wahoos and contained up to 20 calls per individual and context. Some of the acoustic parameters listed in the Appendix (F_0 mean and all parameters describing the structure of the hoo) could not be determined for every call; there were only 193 of the 229 calls for which there were no missing values. Since we aimed to retain as many calls by as many different males as possible in the analysis, we first performed a test run with these 193 calls. We found that F_0 and the variable describing the spectral characteristics of the hoo did not play a role in the discrimination of contexts. We then reverted to the entire data set of 229 calls and excluded these parameters from the analysis. To examine the differences within the contest condition, we raised the number of calls in the analysis so that the maximum number of calls for each male and subcontext was 20. The total number of calls in this analysis was 262 (see Table I for the distribution of calls across individuals and subcontexts).

For analyses in relation to age and context (Table II), we calculated the individual means of ten variables: noise, formant dispersion, mean fundamental frequency, wa duration, hoo duration, amplitude ratio wa/hoo, start and mean first quartile of the distribution of frequency amplitudes, mean first dominant frequency band, mean peak frequency. Finally,

Age class	Contest	Alarm	Contact
Adult	11	7[a]	2[b]
Subadult	4	3[c]	3
Adolescent	1	1	1

[a]Six individuals also represented in the contest category.
[b]One individual also represented in contest and alarm, one individual in the contest category.
[c]One individual also represented in the contest, one individual in the contact, and one individual in the contest and contact category.

to compare the calls of males and females, we used the individual means of 20 acoustic variables that could be determined for both sexes (see the Appendix).

III. RESULTS

A. Acoustic characteristics of alarm and contest wahoos

To test whether contest and alarm wahoos are acoustically different, we first conducted a discriminant function analysis with ''context'' as the grouping variable on 229 calls recorded from 12 males (see Table I). Of the 168 contest calls, 37 were given during male–male chases, 74 were recorded during the morning chorus or when a new male had entered the group, and 57 while herding females. We compared these calls to 61 alarm wahoos recorded from seven males. Forty-six of the alarm calls were given to lions, five to cheetahs (*Acinonyx jubatus*), and ten to wild dogs (*Lycaon pictus*). The average correct assignment was 87.3%; a tenfold cross validation yielded an average correct assignment of 82.7%. Figure 3 shows spectrograms of calls that we selected according to the outcome of the acoustic analysis. The spectrograms depict typical exemplars (i.e., calls with a high assignment probability to their respective context category) of
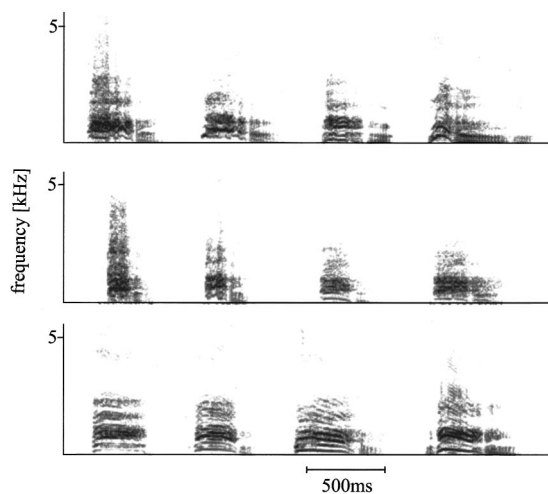

FIG. 3. Spectrograms of wahoo calls from three different males (rows 1–3). For each male, four calls are presented. From left to right: a typical exemplar (according to the outcome of the discriminant function analysis) of an alarm wahoo, an ambiguous exemplar of an alarm wahoo, an ambiguous exemplar of a contest wahoo, and a typical exemplar of a contest wahoo. Note that despite appreciable inter-individual variation, males show structurally similar differences between contexts.

alarm and contest calls recorded from three different males, as well as acoustically more ambiguous exemplars (i.e., calls with a low assignment probability).

Those variables that—according to the discriminant function analysis—contributed most to a discrimination of contexts were the start of the first quartile of the distribution of frequency amplitudes (univariate analysis of variance with context as fixed factor and subject as random factor; only results for test of differences between contexts are given, since in no case did ''subject'' have a significant effect; $F_{1,17} = 17.9$, $P < 0.01$), hoo duration ($F_{1,17} = 13.3$, $P < 0.05$), mean ($F_{1,17} = 4.7$, $P < 0.1$) and minimum first dominant frequency band ($F_{1,17} = 18.4$, $P < 0.01$), and the amplitude ratio wa/hoo ($F_{1,17} = 8.5$, $P < 0.05$; see Table III for more detailed statistics. Note that the inclusion of subject as a factor yields slightly different P levels than in the analysis reported in Table III). In general, contest wahoos had a wa syllable with lower frequency characteristics, a longer hoo duration, and a relatively louder hoo syllable than alarm wahoos. Males also gave alarm and contest wahoos at significantly different rates. While alarm wahoos were given at an $\bar{x} \pm$ s.d. rate of 4.3 ± 1.1 calls/min, contest wahoos occurred at a rate of 30.5 ± 4.0 calls/min (repeated samples with missing values test: $M = 19.6$, $N = 13$, $P < 0.01$).

An inspection of spectrograms suggested that features diagnostic of nonlinear phenomena did not map systematically onto the classification of calls. Across individuals, 25% $\pm 28\%$ ($\bar{x} \pm$ s.d.) of all contest wahoos and 16% $\pm 15\%$ of all alarm wahoos exhibited signs of nonlinear phenomena, mostly in the middle third of the wa syllable (e.g., Fig. 3, row 3, second and fourth call from left). This difference was not significant (repeated samples with missing values test: $M = 1.05$, $N = 12$, n.s.).

B. Differences within the contest category

We found only slight differences among contest wahoos given in the three subcontexts: the average correct assignment to the three subcontexts was 65.6% (tenfold cross validation 48.5%). The parameter contributing most to the discrimination of groups was the mean first quartile of the distribution of frequency amplitudes and the start of the first dominant frequency band. However, subsequent univariate analyses of variance yielded no significant differences in any of the parameters.

C. Effects of age and context

Because we also wished to explore how contact calls compared to alarm and contest wahoos, we conducted a renewed analysis on the individual means of ten acoustic variables (see Sec. II E). However, since only few subjects contributed contact calls, we decided to include contact calls from all age classes (see Table III). Therefore, we ran an analysis in which we explored the influence of age and context simultaneously, and in which we also aimed to identify possible interactions between the factors. Figure 4 shows spectrograms of calls given by males of the three age classes in the three contexts under consideration. Since the variable amplitude ratio wa/hoo had some missing values due to the

TABLE III. Mean±s.d. and results (P-values) of univariate analyses of variance for the variables in the analysis regarding the effects of age and context, including alarm, contest, and contact wahoos from males of all three age classes n.s.: >0.1. The amplitude ratio wa/hoo had to be excluded due to missing values; the mean of the first dominant frequency band was excluded due to a significant univariate interaction.

Acoustic variable	Age class	Context			Statistical effects	
		Contest	Contact	Alarm	Age	Context
Formant disp. [Hz]	Adult	916±58	917±0	875±51	0.003	n.s.
	Subadault	906±83	913±64	984±133		
	Adolescent	996	1036	1197		
Fundamental [Hz]	Adult	312±36	297±9	329±56	0.001	n.s.
	Subadult	341±48	392±91	408±80		
	Adolescent	397	490	430		
Noise [%]	Adult	56±20	24±2	63±15	n.s.	n.s.
	Subadult	53±12	44±47	68±15		
	Adolescent	42	52	31		
'Wa' duration [ms]	Adult	351±47	472±66	322±89	0.001	0.09
	Subadult	285±78	297±81	213±16		
	Adolescent	277	323	278		
'Hoo' duration [ms]	Adult	210±64	214±77	116±62	0.001	0.084
	Subadult	98±48	113±61	34±17		
	Adolescent	0	70	0		
dfal start [Hz]	Adult	432±74	397±12	544±62	0.001	0.001
	Subadult	485±37	549±129	743±103		
	Adolescent	597	526	910		
dfal mean [Hz]	Adult	682±54	668±47	691±40	0.002	0.074
	Subadult	689±35	730±121	816±100		
	Adolescent	775	870	893		
pf mean [Hz]	Adult	755±70	742±48	735±44	0.005	n.s.
	Subadult	753±50	867±140	836±170		
	Adolescent	888	988	914		

absence of the hoo syllable in two of the adolescent males, we had to remove this variable from the analysis. Using the remaining nine variables, we observed significant multivariate differences among contest, alarm, and contact wahoos (Wilk's $\lambda=0.138$; $F_{18,30}=3.00, P<0.01$) and in relation to age (Wilk's $\lambda=0.152$; $F_{20,30}=2.78$, $P<0.01$), but no significant multivariate interaction (Wilk's $\lambda=0.108$; $F_{36,61.69}$

$=1.39$, n.s.). However, subsequent inspection of single variables revealed a significant interaction for the mean first dominant frequency band. This variable was therefore excluded from further consideration (Zar, 1999). All other variables in the analysis except for "noise" varied significantly in relation to age (Table III). Both the mean frequency and the formant dispersion decreased with age, whereas wa and hoo duration increased (Fig. 5). Wa duration, hoo duration, and mean and start of the first quartile of the distribution of frequency amplitudes also varied significantly or marginally significantly in relation to context (Table III). *Post hoc* tests
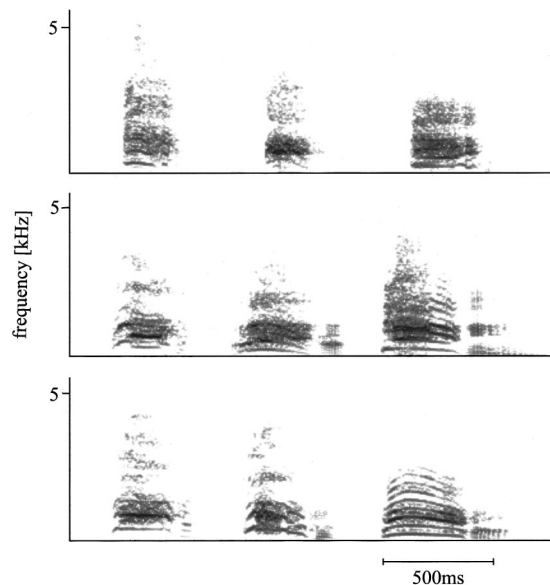

FIG. 4. Spectrograms of wahoo calls from males of three different age classes, given in three different contexts. From left to right: adolescent, subadult, adult. Top row: alarm calls, middle row: contest calls; lower row: contact calls.
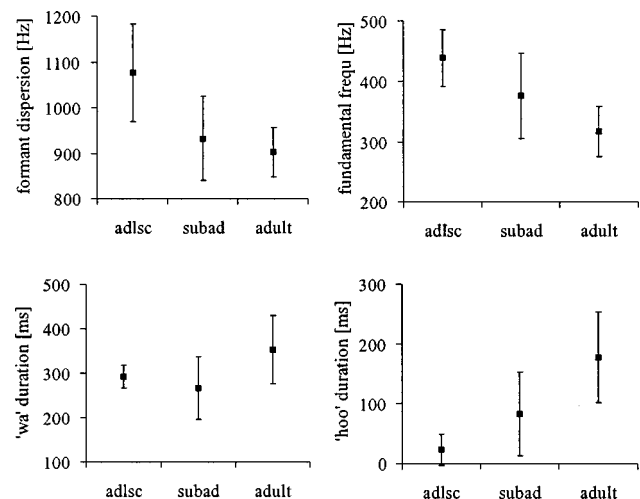

FIG. 5. $\bar{x}\pm$s.d. of four variables that vary in relation to age: formant dispersion, fundamental frequency, wa duration, and hoo duration.

revealed that the hoo duration and the mean first dominant frequency band varied significantly between contest and alarm wahoos, while the start value of the first quartile of the distribution of frequency amplitudes varied significantly between contest and alarm, as well as between contact and alarm wahoos.

For some variables, these effects were limited to specific age groups. For instance, the hoo duration in adolescent contest calls was equivalent to the one in adolescent alarm calls. In sum, we found clear differences in relation to age. Also, across age classes we found consistent differences between alarm and contest wahoos (albeit weaker effects than when the calls of adult males were analyzed separately), and slight differences between alarm and contact wahoos. We failed to find significant differences between contest and contact wahoos. However, due to the small sample size and, as a consequence, the lack of power of this analysis, we cannot rule out the possibility that differences between contest and contact wahoos do exist. Interestingly, we observed a marked difference in the rate at which calls from these two categories were given. Contact calls were given at a much lower rate: 6 of the 14 calls in our sample were given singly, and the remaining calls were given at a rate of 1.5 calls/min (range 0.2–2.4 calls/min).

To make sure that these results also held for a more balanced sample, we replicated this analysis for the calls of adult and subadult males, and included only alarm and contest calls. In this analysis, we also included the amplitude ratio wa/hoo. We observed similar significant multivariate differences in relation to age (Wilk's $\lambda=0.208$; $F_{10,15}=5.72, P<0.001$) and context (Wilk's $\lambda=0.098$; $F_{20,30}=3.28, P<0.01$), and no significant multivariate interaction (Wilk's $\lambda=0.452$; $F_{20,30}=0.73$, n.s.). All variables (see Sec. II E) except formant dispersion varied significantly in relation to age, while wa duration, hoo duration, start and mean first dominant frequency band varied in relation to context. These results support the findings of our previous analysis of all three contexts and age classes.

D. Individual differences

In the analysis of individual differences, we only considered males that contributed at least 16 calls. The data set consisted of 170 calls from eight adult males (16–24 calls per male). Calls were recorded from all major context categories (alarm, contest, and contact). We then repeated this analysis for contest wahoos only (124 calls). We did not have enough alarm or contact wahoos to permit a meaningful separate analysis. The assignment procedure of the discriminant function yielded an average correct assignment of 71.2% (cross validated 59.2%; prior probability 12.5%). The parameters that contributed most to a discrimination of individuals were start first quartile of the distribution of frequency amplitudes (one-way ANOVA $F_{7,169}=17.2, P<0.001$), wa duration ($F_{7,169}=14.3, P<0.001$), and hoo duration ($F_{7,169}=12.6, P<0.001$). However, using discriminant function analysis, all parameters were necessary to distinguish among individuals. If we only considered contest wahoos, the results were essentially replicated: the correct
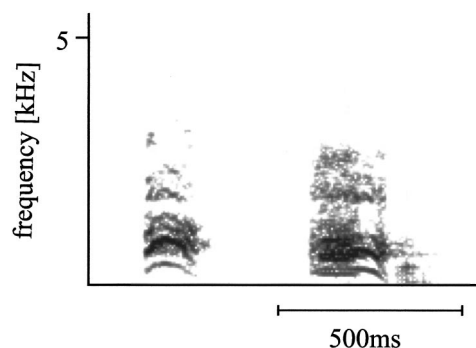

FIG. 6. Spectrograms of a female (left) and a male (right) alarm call.

average assignment was 71.8% (cross validated 58.3%) with 124 calls. The same parameters contributed most to distinguishing among males.

E. Differences between males and females

First, we compared the acoustic structure of the wa syllable of the male alarm wahoo to its equivalent call in adult females, the single-syllable alarm bark. We used only calls that were given in response to lions. For each individual, we calculated the mean value for those acoustic parameters that were common for both sexes (for details on female alarm calls, see Fischer *et al.*, 2001a). There were nine females and seven males represented in this analysis. The acoustic structure of males' and females' alarm calls varied significantly ($F_{1,14}=376.6, P<0.05$). Figure 6 presents spectrograms of a male and a female alarm call. Males exhibited lower frequency characteristics and a longer call duration than females. A variety of parameters that influence perceived pitch varied significantly in relation to sex, for instance the difference between the first and second dominant frequency band, start and mean values of the first dominant frequency band, and the mean first quartile of the distribution of frequency amplitudes (Table IV).

Next, we investigated whether male and female alarm and contact calls varied in similar ways. We found some similarities in male and female calls with regard to the variables that contribute most to a discrimination of alarm and contact calls. For instance, in both sexes, the start of the first quartile of the distribution of frequency amplitudes revealed higher values for alarm calls than for contact calls (mean ±s.d. for female alarm calls: 774±92 Hz; female contact calls: 569±70 Hz; Wilcoxon matched-pairs signed rank test, $n=16$, $z=-3.46, P<0.001$: for male alarm calls 544 ±62 Hz; male contact calls 397±12 Hz, for statistics see Table III). Also, in terms of the call duration, alarm calls

TABLE IV. Statistics ($\bar{x}+$ s.d.) and results of univariate analyses of variance for those variables that vary in relation to sex.

Variable	males	Females	$F_{1,14}$	$P<$
dfb mean difference [Hz]	274±14	357±19	94.8	0.001
dfbl start [Hz]	350±57	473±41	25.8	0.001
dfal mean [Hz]	691±41	824±69	20.5	0.001
dfal start [Hz]	544±63	754±131	15.1	0.005
Duration [ms]	297±77	193±46	14.1	0.005

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were shorter than contact calls for both females and males (female alarm calls 194±46 ms; contact calls 291±42 ms, $z = -3.51, P < 0.001$; male alarm calls: 322±89 ms, contact calls 472±66 ms). Female alarm calls were significantly noisier than contact calls (female alarm calls 62±21%; contact calls 38±15%, $z = -2.94, P < 0.05$; male alarm calls: 63±15%, contact calls 24±12%).

IV. DISCUSSION

A. Acoustic variation in relation to context

Despite their superficial acoustic similarity, alarm and contest wahoos given by adult male baboons exhibit a number of significant acoustic differences. Contest wahoos are given at a much higher rate, exhibit lower frequency characteristics, have a longer hoo duration, and a relatively louder hoo portion than alarm wahoos. Within the different contest contexts, there are only slight differences that do not reach statistical significance. We failed to identify significant differences between contest and contact wahoos in terms of their acoustical structure. However, due to the small sample size, this result should be treated with caution. Contact and contest wahoos clearly differ in terms of the rate at which they occur.

Wahoos also exhibit significant differences among individuals that potentially allow conspecific listeners to identify which male is calling. Similar individual differences have been documented for a variety of other baboon vocalizations, including female grunts (Owren *et al.*, 1997) and alarm barks (Fischer *et al.*, 2001a). Playback studies have shown that these differences are perceptually salient to conspecifics (Fischer *et al.*, 2000; Palombit *et al.*, 1997; Rendall *et al.*, 2000).

We were puzzled by the finding that alarm and contest wahoos represent variations of the same general call type despite the fact that they serve markedly different functions. The same is true for female baboon barks, where "clear" and "harsh" bark variants function as contact and alarm calls, respectively. Overall, baboons appear to produce only a limited number of different call types, the most common of which are tonal, low-frequency grunts (Owren *et al.*, 1997), noisy screams, and pant barks given in submissive interactions or in response to aversive stimuli such as snakes (personal observation). Additionally, females utter mating calls which consist of a drawn-out tonal component and a series of rhythmic pants, while infants may emit tonal "begging" calls.

Why would calls that serve different functions be so similar acoustically? Alarm and contest wahoos may differ only subtly in their acoustic features because they are manifestations of a similar underlying internal state. Predator encounters and male competitive interactions certainly seem to be highly charged contexts that are associated with high states of arousal, and these states may be sufficiently similar that they result in similar-sounding calls. If this affect-based hypothesis is correct, however, it must also account for the subtle but consistent acoustic difference between alarm and contest wahoos—presumably by suggesting that a caller's internal state in these two contexts, while broadly similar, is nonetheless subtly different as well.

Contest and alarm wahoos might also be similar because of limitations in vocal production. The acoustic structure of nonhuman primate calls is determined by oscillation of the vocal folds (and sometimes the vocal lip, see Mergell *et al.*, 1999 for details), articulatory gestures that influence the filtering characteristics of the vocal tract (Brown and Cannito, 1995; Hauser *et al.*, 1993; Hauser and Schön Ybarra, 1994), and respiration (Häusler, 2000). With the present data, we are unable to estimate the influence of the different components. Current evidence suggests that, in nonhuman primates, the anterior cingulate cortex serves to control the initiation of vocalizations, facilitating voluntary control over call emission and onset (Jürgens, 1995). However, the motor coordination of the vocalization appears to take place in the reticular formation of the lower brainstem (Jürgens, 2001), suggesting little voluntary control over the precise structure of the vocal pattern. Thus, contest and alarm wahoos could be linked as well to quite different internal states that converge on similar motor programs (Düsterhoft *et al.*, 2000). Due to methodological constraints, we are currently unable to resolve this question.

B. Acoustic variation in relation to body size

Our findings support the view that animals of bigger size are able to produce longer calls, as males' wa syllables are indeed significantly longer than females' barks. Likewise, we found support for the assumption that large differences in body size lead to differences in fundamental frequency (Darwin, 1872; Morton, 1977): in male wahoos, the fundamental frequency is significantly lower in adults than in younger males or in females. Because we were unable to obtain measurements of adult male body size, it was impossible to determine whether the minimum fundamental is correlated with body size among adults. Studies in adult humans (Fitch and Giedd, 1999) and red deer (McComb, 1991), however, suggest that such a clear correlation is not necessarily the case. Formant frequencies may also serve as reliable indicators of body size, at least across sex and age classes: we observed that formant dispersion decreases with size, but it remains unresolved whether this relation also holds within a given sex and age class. In sum, the loud calls of baboons provide multiple cues to gross size differences. Whether these cues are also reliable within adult males remains an empirical issue. Current theory predicts that the formant frequencies should accurately reflect body size among adult males, whereas fundamental frequency may be less reliable (Fitch and Hauser, in press).

In addition to conveying information about the signaler's body's size, wahoos may also function to advertise a male's endurance and stamina. It seems likely that the hoo syllable represents an exaggerated acoustic trait. This view is supported by the fact that this portion of the call emerges in adolescent males and becomes longer and louder with age, and disproportionately so in contest (and possibly contact) contexts. Further analyses on the relationship between hoo duration and indicators of male stamina within the group of adult males are clearly needed. Further support for the hypothesis that wahoos advertise male quality comes from the fact that, on average, contest wahoos are given at more than five times the rate of alarm wahoos.

C. Listeners' assessment of alarm and contest wahoos

It may seem puzzling at first that calls serving markedly different functions are acoustically so similar, even though they are broadcast over large distances where there may be a cost to ambiguity (Marler, 1965). Given that vocal production in nonhuman primates is heavily constrained (Jürgens, 1995), listeners seem to be under strong selective pressure to differentiate between calls that signal the presence of a predator and those that signal potential aggression. Although call rate varies clearly between alarm and contest wahoos, experiments currently underway suggest that listeners are able to discriminate between these two call types regardless of the rate at which they are presented (D. Kitchen, D. L. Cheney, and R. M. Seyfarth, unpublished data, 2001).

It seems probable that listeners learn to identify those acoustic features that are correlated with each call type, or individual. Infant baboons, for example, appear to learn the distinction between females' contact and alarm barks during development, and their responses to each of these call types becomes more distinctive over time (Fischer *et al.*, 2000). Similarly, through processes of association, and perhaps also by observing the responses of others, listeners attending to wahoos may learn when to escape into trees, when to adopt cryptic positions in order to avoid male aggression, and when it is safe simply to ignore a call.

APPENDIX: ACOUSTIC PARAMETERS CALCULATED FOR THE "WA" SYLLABLE

Variables used for comparison between males and females are indicated by an asterisk.

Parameter	Description
noise [%]*	percent of time segments in which no harmonic structure could be detected
Dfa1 start [Hz]*	frequency at which the distribution of frequency amplitudes reaches the first quartile at beginning of the call
Dfa1 mean [Hz]*	frequency at which the distribution of frequency amplitudes reaches the first quartile, mean across time segments
Dfa2 mean [Hz]*	frequency at which the amplitude distribution reaches the second quartile, mean across time segments
Dfb1 start [Hz]*	first dominant frequency band, at beginning of the call
Dfb1 max [Hz]*	maximum value of dfb1 in all time segments
Dfb1 mean [Hz]*	mean dfb1 across all time segments
Dfb1 minimum [Hz]	minimum value of dfb1 across all time segments
Dfb1 max location	relative position of maximum in the call; ranges between 0 and 1
Db1 slope*	slope of the trend of the dfb (i.e., the linear regression determined by the least squares method)
dfb trend difference [Hz]	mean difference between regression function and actual value of the dfb
dfb3 %*	percentage of time segments with a third dominant frequency band
dfb max difference [Hz]	max difference between first and second dominant frequency band
dfb mean difference [Hz]*	mean difference between first and second dominant frequency band across all time segments
dfb number*	mean number of dominant frequency bands detected in call
dfb ratio*	amplitude ratio between dfb1 and dfb2 (dfb1/dfb2)
fls1 [Hz]*	mean frequency range of first formant-like structure
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 across all time segments
pf mean [Hz]	mean of the frequencies with the highest amplitude across all time segments
pf max [Hz]*	frequency of the maximum frequency of the peak frequency across time segments
pf amplitude max [Hz]	frequency of the maximum amplitude of the peak frequency across time segments
pf max location [Hz]	relative position of maximum in the call; ranges between 0 and 1
pf jump [Hz]*	max difference of the pf in two consecutive time segments
pf slope*	slope of the trend of the pf
pf trend difference [Hz]	mean difference between trend line and pf
pf max jump location	relative location of the max. difference in peak frequency between two adjacent time segments

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