

Do acoustic features of lion, *Panthera leo*, roars reflect sex and male condition?

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(Received 1 November 2006; revised 14 March 2007; accepted 14 March 2007)

Long distance calls function to regulate intergroup spacing, attract mating partners, and/or repel competitors. Therefore, they may not only provide information about the sex (if both sexes are calling) but also about the condition of the caller. This paper provides a description of the acoustic features of roars recorded from 18 male and 6 female lions (*Panthera leo*) living in the Serengeti National park, Tanzania. After analyzing whether these roars differ between the sexes, tests whether male roars may function as indicators of their fighting ability or condition were conducted. Therefore, call characteristics were tested for relation to anatomical features as size, mane color, or mane length. Call characteristics included acoustic parameters that previously had been implied as indicators of size and fighting ability, e.g., call length, fundamental frequency, and peak frequency. The analysis revealed differences in relation to sex, which were entirely explained by variation in body size. No evidence that acoustic variables were related to male condition was found, indicating that sexual selection might only be a weak force modulating the lion's roar. Instead, lion roars may have mainly been selected to effectively advertise territorial boundaries. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2722507]

PACS number(s): 43.80.Ka, 43.80.Jz [JAS]

Pages: 3947–3953

I. INTRODUCTION

Long distance calls provide information about the location of the caller(s) and hence are assumed to serve intergroup spacing (e.g., Mitani, 1985, 1988, 1994; Mitani and Nishida, 1993; Notman and Rendall, 2005; Wilson *et al.*, 2001). In the case of several animals calling at the same time, they may also transmit information about party size (lions: Grinnell *et al.*, 1995; Grinnell and McComb, 1996; McComb *et al.*, 1994; chimpanzee: Wilson *et al.*, 2001). Although in some species females also produce long distance calls (e.g., African elephant: Langbauer *et al.*, 1991; McComb *et al.*, 2003; Poole *et al.*, 1988; Gibbons: Dallmann and Geissmann, 2001; Zebra finches: Cynx and Gell, 2004; Bengalese finches: Kobayasi and Okanoya, 2003; Arctic foxes: Frommolt *et al.*, 2003; lions: McComb *et al.*, 1994), long distance calls are more commonly uttered by males only, presumably serving to attract mates and/or repel competitors. In a diverse range of taxa including birds, amphib-

ians, and mammals, males have been found to produce loud, repetitive calls that apparently function as displays of size, condition, or fighting ability (e.g., Clutton-Brock and Albon, 1979; Davies and Halliday, 1978; Fischer *et al.*, 2004; Kitchen *et al.*, 2003; Reby and McComb, 2003). Such calls may provide listeners with accurate information about the signalers' relative competitive abilities. This is the case when the production of such calls is more costly or difficult for individuals in poor condition than for those in good condition, (Grafen, 1990; Zahavi, 1975, but see also Maynard Smith, 1994; Silk *et al.*, 2000; Vehrencamp, 2000). Alternatively, physiological constraints may determine the quality of the signal, as in the case of so-called "index" signals (Vehrencamp, 2000).

In this paper we examine the loud calls or "roars" of lions (*Panthera leo*). Roars are loud, low-pitched vocalizations that are delivered in bouts, which typically last 30–60 s and consist of several soft introductory moans, a series of full-throated roars, and a terminating sequence of grunts (Grinnell *et al.*, 1995; McComb *et al.*, 1994). Figure 1 shows an example of a male lion call. Male and female lions advertise their territory by roaring and they use the numbers of

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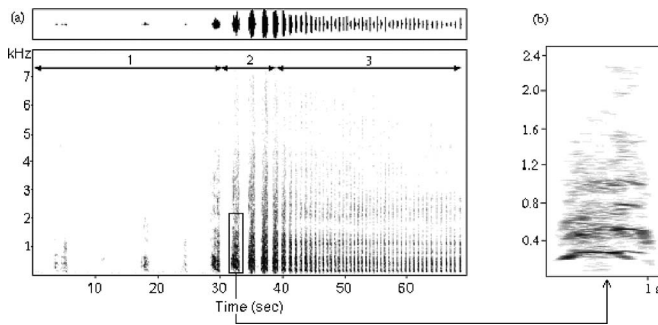


FIG. 1. (a) Spectrogram of a complete male lion call (FFT length: 1024; Frame [%]: 100; Window: Hamming; Overlap: 87.5). The call starts with a series of soft introductory moans (1), followed by a series of full-throated roars (2), and terminates with a sequence of grunts (3). (b) Example of one call unit extracted from the series of full-throated roars (2) (FFT length: 1024; Frame [%]: 100; Window: Hamming; Overlap: 87.5; Sampling frequency: 5000 Hz).

roars they hear to estimate the strength of the opposition (McComb *et al.*, 1994). Roars also function to stay in contact with other pride members, strengthening the bond within the social group, intimidating rivals, and, under certain circumstances, to attract mates (Funston, 1999; Grinnell *et al.*, 1995; Grinnell and McComb, 1996; McComb *et al.*, 1994; Schaller, 1972). Because of their social system, males and females can regularly judge males, and excess females can freely choose among them (West and Packer, 2002). Thus physical properties, like body size and mane length as well as color, might have evolved to signal male genetic and/or phenotypic condition. If that is the case, those characteristics may also be encoded in acoustic call features. Indeed, shorter manes reflect poor fighting ability or short term health, whereas dark manes indicate maturity and high levels of testosterone and nutrition (West and Packer, 2002). Mane darkness influences both female choice and male-male competition. It tends to be a costly signal, because dark-maned males suffer higher surface temperature, abnormal sperm, and lower food intake during the hot months of the year. Nevertheless, because such males tend to be dominant, they enjoy longer reproductive life span and higher offspring survival. Estrous females prefer to mate with males with darker manes while males assess their opponents' mane length and darkness and thereby avoid healthier, older, and more aggressive individuals (West and Packer, 2002).

The purpose of this analysis is to describe the acoustic features of lion roars in detail, and examine (1) whether calls differ between the sexes, and (2) whether, in males, acoustic characteristics are related to anatomical features of the callers. We predicted that larger subjects should produce lower values of spectral parameters (e.g., fundamental frequency, formant dispersion, peak frequency) than smaller bodied animals. Thus, we expected males to differ significantly from females. We also predicted that males with darker and longer manes should exhibit longer calls with more and longer call units. If measures of body size correlate with mane length or color, then dark- or long-maned males should also exhibit low values in the corresponding spectral parameters. The analysis presented below is based on a relatively small number of subjects; however, we would like to highlight that

these kinds of data, including measurements from anaesthetized males, estimates of male length and color, as well as recordings, are extremely difficult to collect.

II. METHODS

A. Subjects and study site

We studied 24 lions (18 males and 6 females), living in the Serengeti National Park, Tanzania. All subjects were individually identifiable from natural markings. Continuous demographic records have been maintained on lions in a 2000-km² study area in Serengeti National Park since 1975 (Packer *et al.*, 1988; Schaller, 1972).

B. Anatomical measurements

In the context of previous studies of Packer and colleagues, animals were anesthetized using 200–500 mg Telazol. Chest circumference was measured using a commercial measuring tape positioned immediately behind the forelegs. For each measurement the accuracy was 1 cm. IACUC (International Animal Care and Use Committee) approval was obtained for all conducted immobilizations. Mane characteristics were evaluated using photographs taken of 568 males from 1964 to 2000 (West and Packer, 2002). Most photographs taken from 1964 to 1990 were black and white; color film was used from 1991. Each photograph was graded for length and color by five undergraduate judges who had never seen the animals in the wild. Students graded both the overall color and length of the mane as well as the color and length of individual areas of the mane (chest, forehead, neck, and shoulders). Multiple images of the same male were evaluated collectively if they were taken within a 1-week period. For each male, the judges' highest and lowest scores were discarded, and the remaining three were averaged. We found no statistically significant effect of picture quality or film type on the judges' scores.

C. Sound recording and analysis

Between October 1984 and December 2000 vocalizations were recorded *ad libitum* using a Panasonic SV 250 portable digital audio tape-recorder or a Sony Professional Walkman WM-D6C as well as a Sennheiser MKH816T directional microphone. Recording distance ranged between 30 and 60 m. In two instances, calls were recorded from 80 and 100 m. While the call recorded at 80 m could only be used for temporal analysis, the "100 m call" appeared to be of sufficient quality for temporal and spectral analysis. Digital recordings were either transferred into a 1990s vintage Macintosh computer using built-in digitizer and Soundedit 16 software or to a PC using an optical wire and USB wave converter (U2A Waveterminal, EGO SYSTEMS Inc.). Recordings were saved in mono format, 16-bit resolution, and 44.1 kHz sampling rate using CoolEdit 2000 (Syntrillium, Phoenix, AZ) software. A total of 33 recordings were available from 24 individuals, and 30 calls were of sufficient quality to permit spectral analysis, i.e., they were not disturbed by background noise such as bird song or the roars of additional lions. Nine of the 33 recordings were missing

some or all of the introductory moans, but the middle part as well as the terminating sequence were still available. Although we included these calls in the spectral analysis, they could not be included in the temporal analysis.

The temporal analysis was conducted using the program Avisoft SASLab Pro 3.92. The start and end of each unit were visually identified and marked. Using these marks, the program automatically calculates various temporal variables. In the complete recordings, we measured the total call duration, number of call units, and average unit duration. Data were stored into a log file and later transferred to a spreadsheet for further analysis.

For spectral analysis we chose the two call units with the highest amplitude from the full-throated roars. This selection was done because differences in the call structure should especially be reflected in those pronounced roar units. Since most of the energy is located in the lower frequencies, by reducing the sampling frequency to 5000 Hz (corresponding to a frequency range of 2500 Hz) we concentrated our analysis to this most interesting area. Calls were down-sampled using the program Avisoft SASLab Pro 3.92. We then extracted the source- (fundamental frequency) and filter- (formant) related acoustic features using PRAAT 4.0.41 (<http://www.praat.org>) and SpeechStation2 (Sensimetrics, Somerville, MA). To calculate the fundamental frequency, PRAAT uses an autocorrelation method described by Boersma (1993). Time step in this analysis was 100 ms. In order to increase the accuracy of the output results by limiting the number of “octave jumps,” we specified the frequency range in which the fundamental frequency was predicted using the pitch settings command. The forecast of the fundamental frequency ranged between 100 and 350 Hz. The limits of this range were determined by visually inspecting the calls. Since fundamental frequency varies within a call unit, we calculated its minimum, maximum, and mean value. In order to determine formant frequencies we conducted a linear predictive coding (LPC) analysis using SpeechStation2 (Sensimetrics, Somerville, MA). LPC analysis is based on assumptions about the source characteristic, which was extensively studied in humans (e.g., Fant, 1960; Liebermann and Blumstein, 1988). While conducting the LPC analysis our study, and in fact all other formant determining studies on animals (e.g., nonhuman primates: Owren *et al.*, 1997; Rendall, 2003; Rendall *et al.*, 2004; dogs: Riede and Fitch, 1999; red deer: Fitch and Reby, 2001; Reby and McComb, 2003), assumed that the source characteristics of humans and the species under examination are not fundamentally different. To our knowledge, no study exists examining the source and filter characteristics and its interaction in lions. We checked the proposed formant frequencies by superimposing them on a corresponding 512-point fast Fourier transformation (FFT) of the same time slice and found that the formants identified were effectively equivalent to the fundamental frequency and the harmonics. Therefore, the LPC did not provide additional information and we refrained from a further evaluation of the formant frequencies. In addition, we carried out a fast Fourier transformation (1024-pt FFT, time step: 5 ms, frequency range: 2500 Hz, frequency resolution: 4.9 Hz) using Avisoft SASLab Pro 3.92. We submitted the

TABLE I. Calculated acoustic variables. Variables marked with “*” were used for statistical analysis.

Acoustic variable	Unit	Description
call duration*	s	time from beginning to end of call
unit #*		number of call units
unit duration*	s	average unit duration of all units in a complete call
F0min*	Hz	minimal fundamental frequency
F0mean*		mean fundamental frequency
F0max*		maximal fundamental frequency
F1	Hz	first formant
F2	Hz	second formant
DF*	Hz	distance between the first and second formant
DFA2 mean*	Hz	frequency at which the amplitude distribution reaches the 2 nd quartile, mean across time segments
DFB2mean*	Hz	Frequency of the second dominant frequency band
PF mean*	Hz	mean of the frequencies with the highest amplitude across all time segments

resulting frequency time spectra to the custom software program LMA 8.4 that extracts several acoustic parameters from the signal (Hammerschmidt, 1990). In order to describe additional spectral features of the roar we assessed parameters describing the distribution of the amplitude in the frequency spectrum. This is done by first determining the overall amplitude for each time segment. Subsequently, we assessed the mean frequency at which the distribution of the amplitude in the frequency spectrum reaches 50% (DFA2mean) of the total distribution. Second, we calculated a parameter that describes the location of the second dominant frequency band (DFB2mean). The dominant frequency bands are characterized by amplitudes that exceed a given threshold in a consecutive number of frequency bins. Note that the number of DFBs count from the lowest frequency up; the first DFB is not necessary the DFB with the highest amplitude. Additionally, we determined the location of the mean peak frequency (PFmean), the frequency with the highest amplitude in a certain time segment. A description of the algorithms is given in Schrader and Hammerschmidt (1997). A summary of calculated acoustic features can be found in Table I. For a schematic representation of DFA, DFB, and PF, see Fig. 2.

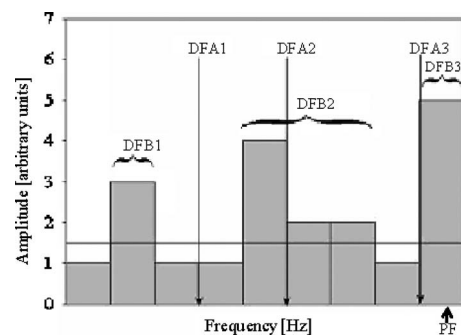


FIG. 2. Schematic representation of variables determined using LMA 8.4 (Hammerschmidt, 1990). DFA: frequency at which the amplitude distribution in the frequency spectrum reaches 25% (DFA1), 50% (DFA2) or 75% (DFA3) of the total value. DFB: frequency of the dominant frequency bands (here: DFB1, DFB2, DFB3) characterized by amplitudes exceeding a given threshold (in this example: 1.5 dB). PF: frequency of the highest amplitude.

D. Statistical analysis

Temporal and spectral parameters of each analyzed call were averaged within each subject. With the exception of the predictor variables chest circumference, mane length, and mane color, all data were normally distributed (normal distribution was determined by visually inspecting histograms and Q-Q Plots). To test whether or not acoustic features vary with sex, we conducted a univariate general linear model using sex as fixed factor. To investigate if physical properties of males (chest circumference, mane length, mane color) influence acoustic features, we carried out a univariate analysis using physiological measurements as covariates. The univariate mode was used to avoid problems with multicollinearity of highly correlating variables ($r > 0.7$). Because of missing values we had to perform the univariate analysis separately for each predictor variable. Subsequently we tested for an overall statistical effect using Fisher's omnibus procedure (Quinn and Keough, 2002). Due to differential predictions, we conducted this correction separately for the influence of sex, chest circumference, mane length, and mane color. To test the statistical power of our results a *post hoc* power analysis (G-Power 2.0f, <http://www.psych.uni-duesseldorf.de/aap/projects/gpower>) was conducted. Considering all available individuals, an α error of 0.05, and an effect size of 0.4 the probability of detecting a given effect was 0.46 (critical $F_{(1,22)}=4.3$, $\lambda=3.84$); in other words, our analysis had a relatively low power of detecting significant effects, the implications of which are considered in Sec. IV.

III. RESULTS

Males had a significantly larger chest circumference than females (mean \pm SD males: 122.12 \pm 4.8 cm, females: 103.4 \pm 5.9 cm; Mann-Whitney *U*-Test $U=0$, $N_1=13$, $N_2=5$, $P < 0.001$). The age when recordings were taken did not differ significantly between the sexes (mean \pm SD males: 7.8 \pm 2.0 years, females: 7.7 \pm 2.8 years; $U=50$, $N_1=6$, $N_2=18$, n.s.). Male mane length averaged 1.3 \pm 0.18 (units), and the color 1.24 \pm 0.23 (units). None of the anatomical measurements correlated with one another, and neither did any of these variables correlate with age (mane length versus color, Spearman's correlation coefficient $r_s=0.259$, $P=0.394$, $N=13$; all other analyses $r_s < 0.5$, all $P > 0.2$). An overview of physical features of all individuals is given in Table II.

The average (mean) call duration of lion calls available for analysis was 39 s (SD=17.4), with the longest (95.7 s) and shortest (23 s) call given by a male. The maximum number of call units was 49 and was uttered by a male. On average, call units lasted 0.67 s (SD=0.21). The fundamental frequency in males was on average (mean) 194.55 Hz (SD=26.3) and in females 206.57 Hz (SD=28.67). The first formant was located at 204.9 Hz (SD=35.2) in males and 222.3 Hz (SD=32.5) in females, while the second formant was located at 444.7 (SD=51.7) in males and 500.5 Hz (SD=66.2) in females, respectively.

The Fisher's omnibus test revealed an overall effect of sex ($\chi^2=38.8$, $df=18$, $p=0.003$) on the acoustic structure of roars. Following this effect, the univariate analyses showed significant differences between the sexes for the mean fre-

TABLE II. Overview of physical variables: m=male, f=female.

ID	Sex	Chest circumference (Hz)	Age (year)	Mane length	Mane color
BC4	m	127	11.4	1.46	1.28
CA	m		9.6		
CK	m	121	9.4	1.37	1.58
JO	m	121	6.4	1.54	1.24
M10	m	126	5.8	1.01	1.01
M14	m	126	5.8	1.03	1.19
NO	m	120	9.8		
PL	m	123	10.6		
PN	m	117	7.4	1.46	1.18
PS	m	116	10.3		
SN	m	114	7.5	1.36	1.55
TW	m	120	8.8		
CL5	m	129	5.6	1.50	1.44
OL	m		7.9	1.50	1.16
ME	m	128	6.5	1.38	1.20
VD	m		7.2	1.25	1.26
DO	m		6.5	1.25	1.38
WN	m		4.4	1.08	0.71
G06	f		5.4		
G07	f	102	5.5		
SB	f	113	4.5		
SMC	f	104	10.9		
SY	f	98	10.1		
WO	f	100	9.8		

quency of the second amplitude quartile (DFA2mean), the mean frequency of the second dominant frequency band (DFB2mean), as well as for the minimum fundamental frequency (F0min; see Table III). Males produced lower values than females in all three acoustic features. However, the explained variance was quite low with a corrected R^2 of 0.277 (DFA2mean), 0.262 (DFB2mean), and 0.213 (F0min). All

TABLE III. Results of univariate analyses displaying sex differences in acoustic variable minimal fundamental frequency (F0min), mean fundamental frequency (F0mean), maximal fundamental frequency (F0max), formant dispersion (DF), call duration (call dur), number of call units (unit #), average unit duration (unit dur), mean frequency of the second amplitude quartile (DFA2mean), frequency of the second dominant frequency band (DFB2mean), and peak frequency (PFmean). *F* values, degrees of freedom, and *P* values are displayed. The Fisher's omnibus test revealed an overall significant effect ($\chi^2=38.8$, $df=18$, $p=0.003$). The column "prediction" indicates whether the predictions are met, with males producing lower spectral and longer temporal acoustic values than females. A "+" indicates "yes" predictions are met, while a "-" indicates "no" the relationship is contrary to the predictions.

Fixed factor	Dependent variable	<i>F</i>	Hypothesis df	Error df	<i>P</i>	<i>N</i>	Prediction
Sex	F0min	6.684	1	20	0.018	22	+
	F0mean	0.869	1	20	0.362	22	+
	F0max	0.095	1	20	0.761	22	+
	call dur	1.280	1	17	0.274	19	+
	unit #	0.040	1	17	0.844	19	+
	unit dur	0.58	1	17	0.457	19	+
	DFA2mean	9.044	1	20	0.007	22	+
	DFB2mean	8.473	1	20	0.009	22	+
	PFmean	2.752	1	20	0.113	22	+

TABLE IV. Results of the univariate analyses of chest circumference, mane length, and mane color on acoustic features (legend as in Table III). The Fisher's omnibus test for chest circumference: $\chi^2=33.6$, $df=18$, $p=0.01$; mane length: $\chi^2=25.28$, $df=18$, $p=0.1$; mane color: $\chi^2=26.7$, $df=18$, $p=0.08$. The column "direction/prediction" indicates whether the acoustic variable under examination increases (\uparrow), decrease (\downarrow), or does not show any trend ($-$) with increasing size, mane length or coloration, respectively. A '+' indicates that the predictions are met, while '-' indicates that predictions are not fulfilled.

Covariate	Dependent variable	F	Hypothesis df	Error df	P	N	Direction/prediction
Chest circumference	F0min	2.944	1	10	0.153	12	$\downarrow/+$
	F0mean	2.839	1	10	0.123	12	$\downarrow/+$
	F0max	0.157	1	10	0.700	12	$-$
	call dur	0.669	1	7	0.440	9	$\downarrow/-$
	unit #	1.136	1	7	0.322	9	$\downarrow/-$
	unit dur	1.151	1	7	0.319	9	$\downarrow/-$
	DFA2mean	4.032	1	10	0.072	12	$\downarrow/+$
	DFB2mean	11.158	1	10	0.007	12	$\downarrow/+$
	PFmean	8.135	1	10	0.017	12	$\downarrow/+$
Mane length	F0min	0.173	1	9	0.688	11	$-$
	F0mean	0.005	1	9	0.948	11	$-$
	F0max	4.128	1	9	0.073	11	$\downarrow/+$
	call dur	6.13	1	6	0.048	8	$\downarrow/-$
	unit #	2.499	1	6	0.165	8	$\downarrow/-$
	unit dur	6.244	1	6	0.047	8	$\downarrow/-$
	DFA2mean	0.704	1	9	0.423	11	$\downarrow/+$
	DFB2mean	0.004	1	9	0.951	11	$-$
	PFmean	0.612	1	9	0.454	11	$\downarrow/+$
Mane color	F0min	5.124	1	9	0.050	11	$\uparrow/-$
	F0mean	5.951	1	9	0.037	11	$\uparrow/-$
	F0max	0.732	1	9	0.414	11	$\uparrow/-$
	call dur	0.094	1	6	0.769	8	$-$
	unit #	1.508	1	6	0.265	8	$\downarrow/-$
	unit dur	1.580	1	6	0.255	8	$\uparrow/+$
	DFA2mean	2.252	1	9	0.168	11	$\uparrow/-$
	DFB2mean	0.529	1	9	0.485	11	$\uparrow/-$
	PFmean	0.520	1	9	0.489	11	$\uparrow/-$

other spectral variables showed a trend in the predicted direction (Binomial test: $p < 0.05$). When we controlled for body size (chest circumference), no differences between the sexes remained ($p > 0.2$).

In addition, we examined whether or not features that might be related to male status varied with certain aspects of their vocalizations. The corresponding Fisher's omnibus effect test revealed that chest circumference ($\chi^2=33.6$, $df=18$, $p=0.014$) but not mane color ($\chi^2=26.7$, $df=18$, $p=0.08$) and mane length ($\chi^2=25.28$, $df=18$, $p=0.12$) were related to roar structure (see Table IV). Smaller males produce roars with a higher frequency of the second dominant frequency band (DFB2mean) and a higher peak frequency ($p < 0.02$), and, again, the remaining spectral variables showed a relation with size in the predicted direction. The picture was less clear for mane length and mane color, where some of the trends were in the predicted and some in the opposite direction, supporting the notion that there is a poor correlation between these measures of male status and roar structure.

IV. DISCUSSION

Our analysis revealed significant differences in the structure of male and female lion roars, which, however, could

entirely be explained by differences in body size. The acoustic features of male roars neither varied with mane color nor with mane length. Both mane color and mane length are signals of male status and have been characterized as costly signals, because larger manes and darker hair increase the surface temperature and decrease the rates of heat transfer, which can harm sperm production (West and Packer, 2002). Moreover, previous analyses revealed a correlation between mane length and color with age and testosterone—another costly trait (West and Packer, 2002). Thus, male lions have apparently been subjected to intense sexual selection. Somewhat surprisingly, it seems that sexual selection has not affected the structure of their calls, as the call structure was neither related to signs of male condition nor did they exhibit pronounced differences between the sexes. Notably, the duration of the overall call did not correlate with any of the variables that have been implied in signifying male status; in addition call duration also failed to exhibit significant differences between the sexes. In contrast, high ranking male baboons produce longer bouts of calls than lower ranking baboons (Kitchen *et al.*, 2003). Note that among adult baboons, rank is not related to size. Thus, acoustic variation related to condition is not simply an indicator of subject size.

In terms of the acoustic features, we found that fundamental frequency, the frequency of the second amplitude quartile (DFA2mean) and the second dominant frequency band (DFB2mean) varied between the sexes and thus with the size of the caller. This is in line with other studies indicating that fundamental frequency can be used to assess size differences (e.g., Fischer *et al.*, 2001; Hammerschmidt *et al.*, 2000; Hauser, 1993; Pfefferle and Fischer, 2006). Variation in acoustic structure is salient to listeners: a previous study showed that female lions become agitated, retreating with their cubs (if those reached 4.5 months of age) when presented with roars of unfamiliar males. However, movement towards the loudspeaker was observed after playbacks of unfamiliar female roars. This response difference indicates that female lions are able to identify the sex of the stranger (McComb *et al.*, 1993). Furthermore, while females with cubs remained relaxed on hearing roars from resident males, they immediately become agitated on hearing unfamiliar males, i.e., females with cubs more often retreated with or showed behavior related to cub defense (McComb *et al.*, 1993). This discrimination ability could be mediated by knowledge of the individual call characteristics of pride members.

Within the category of adult males, we found significant differences between peak frequency (PF) and the frequency of the second dominant frequency band (DFB2mean), suggesting information about body size is encoded in the calls and potentially available to listeners. Analysis concerning the relationship between fundamental frequency and body size revealed no correlation. However, the *P* values were rather low (0.15 and 0.12, respectively). In light of the low power, it might therefore be possible that a larger data set would indeed reveal a significant correlation between fundamental frequency and body size.

The fact that female and male roars differ only slightly in terms of their spectral structure, but not fundamentally in terms of their overall structure, raises the question of the primary function of these calls. Possibly, the structure of roars has been selected to effectively advertise territorial boundaries. This hypothesis is supported by the fact that both male and female lions are territorial and use roars to advertise and defend their territory (McComb *et al.*, 1994). Thus, unlike in baboons where only males produce long distance two-syllable calls (“wahoos”) that serve to advertise a male’s fighting ability and stamina (Fischer *et al.*, 2004; Kitchen *et al.*, 2003), the operative selection pressure on lion roaring might have been the same for both sexes. Interestingly, Grinnell and McComb (2001) found that resident males remained silent outside of their territories even when presented with playbacks of unfamiliar males roaring, and nomadic males started roaring only when they took over a pride (Grinnell and McComb, 2001), supporting the view that the primary function of roars is the advertisement and defense of the territory.

Differences in response to male and female calls could be mediated by attending to features related to size differences. However, overall, the lack of differences between male and female lion roars is striking given the fact that, otherwise, this species exhibits signs of strong sexual selection.

ACKNOWLEDGMENTS

We would like to thank Kurt Hammerschmidt for valuable discussion and for kindly making his sound analysis program LMA available.

- Boersma, P. (1993). “Accurate Short-Term Analysis of the fundamental Frequency and the Harmonics-To-Noise-Ratio of a Sampled Sound,” Proceedings of the Institute of Phonetic Science (IFA) **17**, 97–110.
- Clutton-Brock, T. H., and Albon, S. D. (1979). “The roaring of red deer and the evolution of honest advertisement,” *Behaviour* **69**, 145–170.
- Cynx, J., and Gell, C. (2004). “Social meditation of vocal amplitude in a songbird, *Taeniopygia guttata*,” *Anim. Behav.* **67**, 451–455.
- Dallmann, R., and Geissmann, T. (2001). “Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*),” *Behaviour* **138**, 629–648.
- Davies, N. B., and Halliday, T. R. (1978). “Deep croaks and fighting assessment in toads *Bufo bufo*,” *Nature (London)* **274**, 683–685.
- Fant, G. (1960). *Acoustic Theory of Speech Production* (Mouton, The Hague).
- Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (2001). “Acoustic features of female chacma baboon barks,” *Ethology* **107**, 33–54.
- Fischer, J., Kitchen, D. M., Seyfarth, R. M., and Cheney, D. L. (2004). “Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion,” *Behav. Ecol. Sociobiol.* **56**, 140–148.
- Fitch, W. T., and Reby, D. (2001). “The descended larynx is not uniquely human,” *Proc. R. Soc. London, Ser. B* **268**, 1669–1675.
- Frommolt, K. H., Goltsman, M. E., and MacDonald, D. W. (2003). “Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal,” *Anim. Behav.* **65**, 509–518.
- Funston, P. J. (1999). “Predator-prey relationships between lions and large ungulates in the Krüger National Park,” Ph.D. thesis, University of Pretoria.
- Grafen, A. (1990). “Biological signals as handicaps,” *J. Theor. Biol.* **144**, 475–546.
- Grinnell, J., and McComb, K. (1996). “Maternal grouping as a defence against potentially infanticidal males: evidence from field playback experiments on African lions,” *Behav. Ecol.* **7**, 55–59.
- Grinnell, J., and McComb, K. (2001). “Roaring and social communication in African lions: the limitations imposed by listeners,” *Anim. Behav.* **62**, 93–98.
- Grinnell, J., Packer, C., and Pusey, A. E. (1995). “Cooperation in male lions: kinship, reciprocity or mutualism?” *Anim. Behav.* **49**, 95–105.
- Hammerschmidt, K. (1990). “Individuelle Lautmuster bei Berberaffen (*Macaca sylvanus*): Ein Ansatz zum Verständnis ihrer vokalen Kommunikation” (“Individual vocal pattern of Barbary macaques (*Macaca sylvanus*): An approach towards the understanding of their vocal communication”), Ph.D. thesis, FU Berlin, Berlin, Germany.
- Hammerschmidt, K., Newman, J. D., Champoux, M., and Suomi, S. J. (2000). “Changes in rhesus macaque ‘coo’ vocalizations during early development,” *Ethology* **106**, 873–886.
- Hauser, M. D. (1993). “The evolution of nonhuman primate vocalizations: Effects of phylogeny, body weight, and social context,” *Am. Nat.* **142**, 528–542.
- Kitchen, D. M., Fischer, J., Cheney, D. L., and Seyfarth, R. M. (2003). “Loud calls as indicators of dominance in the male baboon (*Papio cynocephalus ursinus*),” *Behav. Ecol. Sociobiol.* **53**, 374–384.
- Kobayasi, K. I., and Okanoya, K. (2003). “Sex differences in amplitude regulation of distance calls in Bengalese finches, *Lunchula striata* var. *domestica*,” *Anim. Biol.* **53**, 173–182.
- Langbauer, W. R., Payne, K. B., Charif, R. A., Rapaport, L., and Osborn, F. (1991). “African elephants respond to distant playbacks of low-frequency conspecific calls,” *J. Exp. Biol.* **157**, 35–46.
- Liebermann, P., and Blumstein, S. E. (1988). *Speech Physiology, Speech Perception, and Acoustic Phonetics* (Cambridge U. P., Cambridge, England).
- Maynard Smith, J. (1994). “Must reliable signals always be costly?” *Anim. Behav.* **47**, 1115–1120.
- McComb, K., Packer, C., and Pusey, A. (1994). “Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*,” *Anim. Behav.* **47**, 379–387.
- McComb, K., Pusey, A., and Packer, C. (1993). “Female lions can identify potentially infanticidal males from their roars,” *Proc. R. Soc. London, Ser. B* **252**, 59–64.

- McComb, K., Reby, D., Baker, L., Moss, C., and Sayialel, S. (2003). "Long-distance communication and acoustic cues to social identity in African elephants," *Anim. Behav.* **65**, 317–329.
- Mitani, J. C., and Nishida, T. (1993). "Contexts and social correlates of long-distance calling by chimpanzees," *Anim. Behav.* **45**, 735–746.
- Mitani, J. C. (1985). "Sexual selection and adult male orangutan loud calls," *Anim. Behav.* **33**, 271–283.
- Mitani, J. C. (1988). "Male gibbon (*Hylobates agilis*) singing behaviour: natural history, song variations and function," *Ethology* **79**, 177–194.
- Mitani, J. C. (1994). "Ethological studies of chimpanzee vocal behaviour," in *Chimpanzee cultures*, edited by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne (Harvard U. P., Cambridge, MA), pp. 241–254.
- Notman, H., and Rendall, D. (2005). "Contextual variation in chimpanzee pant hoots and its implications for referential communication," *Anim. Behav.* **70**, 177–190.
- Owren, M. J., Seyfarth, R. M., and 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.
- Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J., and Borgerhoff-Mulder, M. (1988). "Reproductive success of lions," in *Reproductive Success*, edited by T. H. Clutton-Brock (Univ. of Chicago, Chicago), pp. 363–383.
- Pfefferle, D., and Fischer, J. (2006). "Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*," *Anim. Behav.* **72**, 43–51.
- Poole, J. H., Payne, K., Langbauer, W. R., and Moss, C. (1988). "The social contexts of some very low frequency calls of African elephants," *Behav. Ecol. Sociobiol.* **22**, 385–392.
- Quinn, G. P., and Keough, M. J. (2002). *Experimental Designs and Data Analysis for Biologists* (Cambridge U. P., Cambridge, England).
- Reby, D., and McComb, K. (2003). "Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags," *Anim. Behav.* **65**, 519–530.
- Rendall, D. (2003). "Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalization of baboons," *J. Acoust. Soc. Am.* **113**, 3390–3402.
- Rendall, D., Owren, M. J., Weerts, E., and Hienz, R. D. (2004). "Sex differences in the acoustic structure of vowel-like grunt vocalizations in baboons and their perceptual discrimination by baboon listeners," *J. Acoust. Soc. Am.* **115**, 411–421.
- Riede, T., and Fitch, T. W. (1999). "Vocal Tract Length and Acoustics of Vocalization in the Domestic Dog (*Canis familiaris*)," *J. Exp. Biol.* **202**, 2859–2867.
- Schaller, G. B. (1972). *The Serengeti Lion* (Univ. of Chicago, Chicago).
- Schrader, L., and Hammerschmidt, K. (1997). "Computer-Aided Analysis of Acoustic Parameters in Animal Vocalisations: A Multi-Parametric Approach," *Bioacoustics International Journal of Animal Sound and its Recording* **7**, 247–265.
- Silk, J. B., Kaldor, E., and Boyd, R. (2000). "Cheap talk when interests conflict," *Anim. Behav.* **59**, 423–432.
- Vehrencamp, S. L. (2000). "Handicap, index, and conventional elements of bird song," in *Animals Signals: Signaling and Signal Design in Animal Communication*, edited by Y. Espmark, T. Amundsen, and G. Rosenquist (Trondheim, Tapir), pp. 277–300.
- West, P. M., and Packer, C. (2002). "Sexual Selection, Temperature, and the Lion's Mane," *Science* **297**, 1339–1343.
- Wilson, M. L., Hauser, M. D., and Wrangham, R. W. (2001). "Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees?" *Anim. Behav.* **61**, 1203–1216.
- Zahavi, A. (1975). "Mate Selection - A Selection for Handicap," *J. Theor. Biol.* **53**, 205–214.