



African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers

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The most common vocalization of the African elephant, *Loxodonta africana*, is the rumble, but there is no consensus as to how many rumble subtypes exist. From the standpoint of social function, many types of rumble have been proposed. From a structural standpoint, however, few studies have examined detailed acoustic measurements of a large number of calls. We analysed 270 rumbles from six adult female African elephants housed at Disney's Animal Kingdom (Lake Buena Vista, Florida, U.S.A.). Subjects wore collars outfitted with microphones and radiotransmitters that allowed recording of vocalizations from identified individuals. Rumble vocalizations were digitized and both source and filter features were measured for each call. Behavioural and endocrine data were collected so that acoustical data could be placed into the context of ongoing social behaviour and reproductive state. Multidimensional scaling analysis revealed that, from a structural standpoint, rumbles from this captive setting could not be divided into distinct subtypes, but there was extensive acoustic variation across rumbles. Discriminant function analysis and MANOVA were employed to further explore this variation. First, acoustic characteristics varied according to the individual identity of the caller. Second, rumbles varied as a function of negative emotional arousal. When associating with dominant animals, subordinate females produced rumbles with lower cepstral coefficients, suggesting low tonality and unstable pitch in the voice, compared to rumbles produced outside of the presence of dominant animals. Rumbles as a whole did not cluster into distinct acoustic types, but structural variation in rumbles reflected the individual identity and emotional state of callers.

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The vocalizations produced by an animal species can be categorized from both structural and functional standpoints, and the relationship between the two may take many forms. The African elephant, *Loxodonta africana*, 'rumble' vocalization has been categorized into various subtypes based on its putative social functions, but the analysis of rumbles from a structural standpoint has received considerably less attention. In this paper, we examine the acoustic structure of captive female African elephant rumble vocalizations to shed light on the following questions. (1) Do rumbles fall into morphologically distinct subtypes, or is the observed variation graded in nature? (2) Is the structural variation in rumbles associated with the individual identity, reproductive state or emotional state of the caller?

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When attempting to understand the vocal communication system of another species, the most fundamental task is to delineate its vocal repertoire. Ideally, separate vocalization types will be acoustically distinct from one another, without structural overlap, but within each call type there may be varying degrees of graded variation (Nowicki & Nelson 1990; Bradbury & Vehrencamp 1998). The discrete burst of acoustic energy (i.e. the call) is considered the functional unit of animal vocal communication, but biological significance can be associated with levels both above and below the call (Hauser 2000). For example, complex sequential combinations of calls may constitute functional units of communication, such as the acoustic 'elements', 'syllables' and 'phrases' that make up some male bird songs, which mediate territorial defence and mate attraction (Catchpole & Slater 1995). In addition, structural variation within a call may serve communicative functions, such as the primate 'coo' call, which can vary structurally as a function of social context (Green 1975) or internal state (Bayart et al. 1990).

It is well known that variation in animal vocalizations can reveal membership in biological categories such as population (e.g. water frogs, *Rana lessonae*: Wycherley et al. 2002), sex (e.g. humans: Bachorowski & Owren 1999), kin group (e.g. stripe-backed wrens, *Campylorhynchus nuchalis*: Price 1999) and individual identity (e.g. bottlenose dolphins, *Tursiops truncatus*: Sayigh et al. 1998). Additionally, female vocalizations can signal sexual receptivity (e.g. anurans: Tobias et al. 1998; Emerson & Boyd 1999) and reproductive state in cycling females (e.g. primates: Semple & McComb 2000; Semple et al. 2002). Finally, caller affect can be reflected in the voice through physiological mechanisms (e.g. Scherer 1986; Porges 1995), and in primates, negative emotional arousal has been shown to influence a variety of acoustic changes in voiced sounds, including increased and unstable fundamental frequency (e.g. nonhuman primates: Fichtel et al. 2001; Rendall 2003; humans: Bachorowski & Owren 1995; Bachorowski 1999; Soltis 2004).

There is no strong consensus on the vocal repertoire of the African elephant in general, and no consensus on the number of rumble subtypes in particular. Rumbles are frequency-modulated, harmonically rich vocalizations with frequency components near or within the infrasonic range. In an early study, Berg (1983) classified 209 vocalizations from nine captive elephants into 10 acoustic types, including two separate types of rumble (the 'growl' and 'rolling growl' in Berg's terminology). In the parameters described, however, the two rumbles differ very little, or not at all. Mean durations do differ but they overlap extensively, and the range of fundamental frequencies are the same for the two calls. Among wild elephants, Poole et al. (1988) categorized seven rumble types according to their social function, and provided various acoustic characteristics (e.g. frequency contour characteristics) for exemplars corresponding to each type. Poole (1999) also characterized oestrous rumbles according to measures of the fundamental contour. From these descriptions, however, it is not possible to determine whether these rumble types differ acoustically as discrete subtypes or in a graded manner.

Leong et al. (2003a) analysed 983 vocalizations from two male and six female captive African elephants and categorized them into eight acoustic types, including three types of rumble ('rumble', 'loud rumble', and 'noisy rumble'). Classification was performed from visual inspection of spectrograms, not from quantitative acoustic measurements, so it is unclear to what extent the three rumble subtypes are structurally distinct from one another. The pros and cons of classifying vocalizations on the basis of visual inspections of spectrograms versus computerized techniques have been discussed for chickadees (Nowicki & Nelson 1990) and dolphins (Janik 1999; McCowan & Reiss 2001; Watwood et al. 2004).

In one study, McComb et al. (2003) examined acoustic cues to individual identity using 99 rumble vocalizations from 13 wild, adult female African elephants. Entering nine acoustic variables into a stepwise discriminant function analysis, they were able to classify rumbles of unspecified identity to the correct individual in 53.6 to 77.4% of cases (depending on how conservative was the

analysis). A success rate of only 7.7% (1/13) was expected by chance alone, thus providing the first quantitative evidence that acoustic features of rumbles reflect individual identity in African elephants (also see Clemens et al. 2005).

This paper builds on previous work by making quantitative acoustic measurements on a large set of captive female African elephant rumbles. In this way, we hope to provide evidence as to whether or not rumbles can be divided into distinct subtypes based on acoustic structure alone. We then relate the observed variation to three dimensions of potential biological importance: individual identity, reproductive phase and emotional state of the caller. Finally, we link these structural analyses to previously and newly proposed social functions of the rumble, specifically as such functions relate to social separation, mate attraction and dominance interactions.

METHODS

Study Subjects and Housing

The herd of African elephants consisted of three adult males and seven adult females housed at Disney's Animal Kingdom (DAK), Lake Buena Vista, Florida, U.S.A. Study subjects were six adult nonpregnant, nulliparous females (age range 16–30 years). Subjects were housed in indoor stalls overnight and released into one of two naturalistic outdoor enclosures (main yard: 2.29 ha; small yard: 0.55 ha), or a smaller yard attached to the indoor barn (barn yard: 0.04 ha). We collected vocal and concomitant behavioural data on five females during January–November 2000, and from one additional female in December 2002 (who arrived at DAK in November 2000). The data presented on the first five females are derived from social configurations in which one male and four females were housed in the main yard, or in which no males and all six females were housed in the main yard. Data on the sixth female are derived from configurations in which all seven females and no males were housed in the main yard. One female in the herd did not regularly wear a recording collar and is not included in this analysis.

Vocal Data Collection

Elephant vocalizations were recorded from transmitters mounted in collars worn by the elephants, which have been described elsewhere (Leong et al. 2003a, b; Soltis et al. 2005). Briefly, each collar contained a condenser microphone element, a radiotransmitter with antenna, and a battery pack. Each collar transmitted acoustic data on a unique radio frequency to an antenna-receiver component, each of which was connected to a separate channel of an eight-channel digital audio recorder where they were recorded at a 44.1-kHz sample rate to separate tracks on digital audiotape. On recording days, collars were put on the elephants in the morning and removed at night to recharge batteries. A 1-h tape was recorded each day the collars were worn, always between 1000 and 1400 hours. The vocal data were collected from 83 1-h sessions.

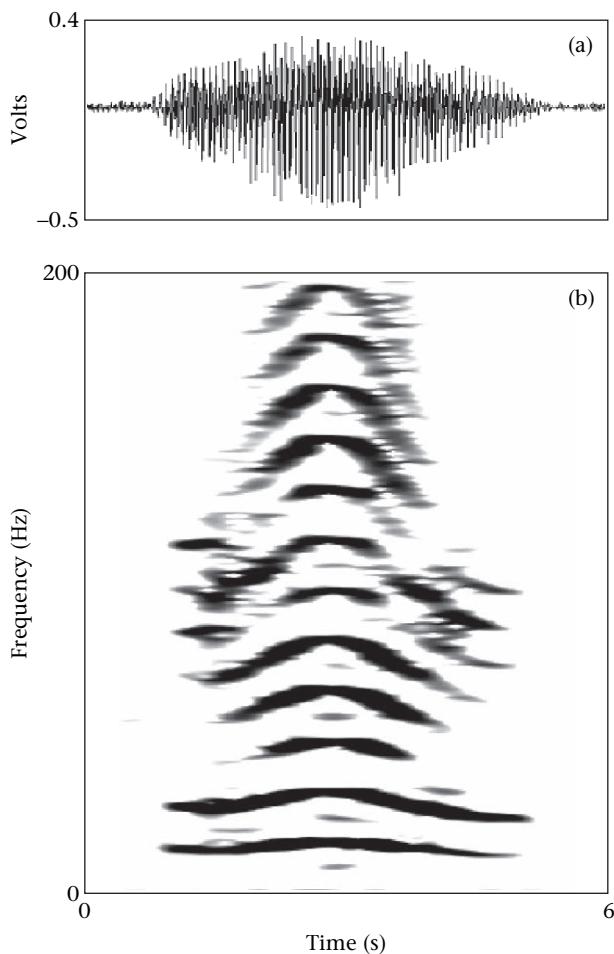


Figure 1. (a) Waveform and (b) spectrograph (512-point fast Fourier transform, Hanning window) of an elephant rumble vocalization. Time–frequency point measures were taken from the spectrograph view and used to calculate measures 1–8 in Table 1.

Vocalization Analysis

Data tapes were played on a DAT recorder (TASCAM DA-38) through an audio mixer (Mackie 1202-VLZ) and an antialiasing filter (Tunable Active Filter Instrument 900C/9L8B 8-pole Butterworth low-pass filter), and vocalizations were located on each channel of the tape using Real Time Spectrogram (RTS; version 2.0, Engineering Design, Berkeley, California, U.S.A.). RTS sample rate was set at 1200 Hz to visually locate vocalizations that contained low-frequency components (i.e. rumble vocalizations). Collar microphones were sensitive enough to pick up vocalizations of nearby elephants. Identification of callers was determined by relative strength and timing of signals using a customized eight-channel Real Time Event Detector at a 1200 Hz sample rate (RTED; Engineering Design) and observation of video (see below). Vocalizations were digitized and saved in RTS at 7500-Hz sample rate.

We performed acoustic measurement of both source and filter features of previously digitized rumble vocalizations with SIGNAL bioacoustics software (version 3.1; Engineering Design). Automated routines were written to perform the following manipulations on previously digitized rumble

vocalizations. Each vocalization was decimated from the 7500-Hz sample rate to a sample rate of 625 or 500 Hz so that low-frequency vocalizations could be viewed (at a 250- and 200-Hz bandwidth, respectively, depending on the analysis). Measures based on time–frequency points across the fundamental were taken from the spectrograph view (Fig. 1). We calculated a power density spectrum over the entire signal to measure mean frequency, and for the middle 100 ms of the call to extract formant frequencies and amplitudes (Fig. 2). We also calculated the second-order transform of the power spectrum, or the ‘cepstrum’, which is a spectrum of a spectrum (Blankenship 2002), over the middle 2 s of each call to measure cepstral peak (Fig. 3). Figures 1–3 were produced in SIGNAL 4.1.

Table 1 shows a complete list of the 16 acoustic measures taken on each call, including features related to vocal fold activity (source features) and vocal tract shape (filter features). Standard time–frequency measures were taken to extract source features and to capture the overall shape of the frequency-modulated vocalizations. Formant frequencies and amplitudes were extracted to measure filter

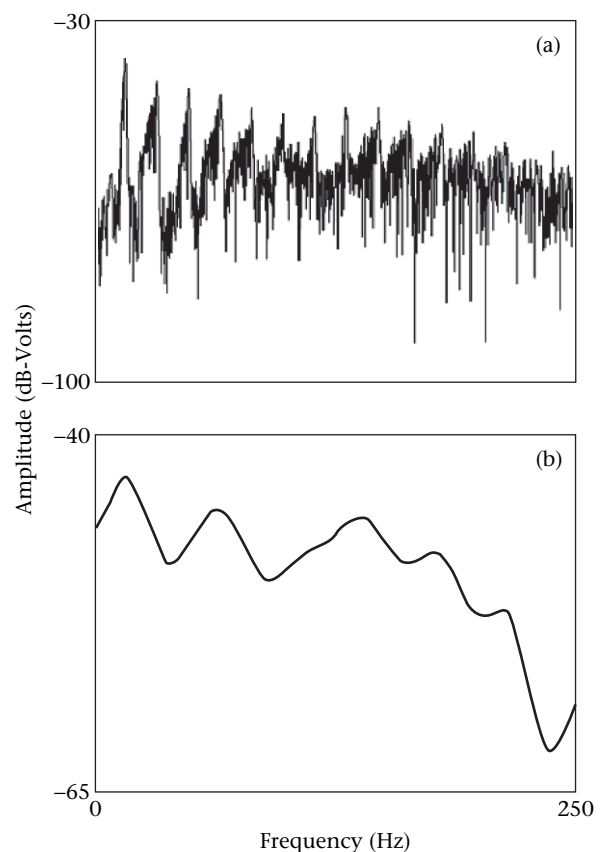


Figure 2. Power density spectra of an elephant rumble. (a) Power spectrum across the whole call showing harmonics (4096-point fast Fourier transform, FFT, Hanning window). (b) Power spectrum for 100 ms beginning at call midpoint showing formants (256-point FFT, Hanning window, smoothed once with a 20-Hz window). Both power spectra are from the rumble shown in Fig. 1. In (a), mean frequency (measure 9 in Table 1) was defined as the frequency at the first peak corresponding to the fundamental frequency. In (b), amplitude and frequency values were taken at the maxima of the first three formant peaks for measures 10–15 in Table 1.

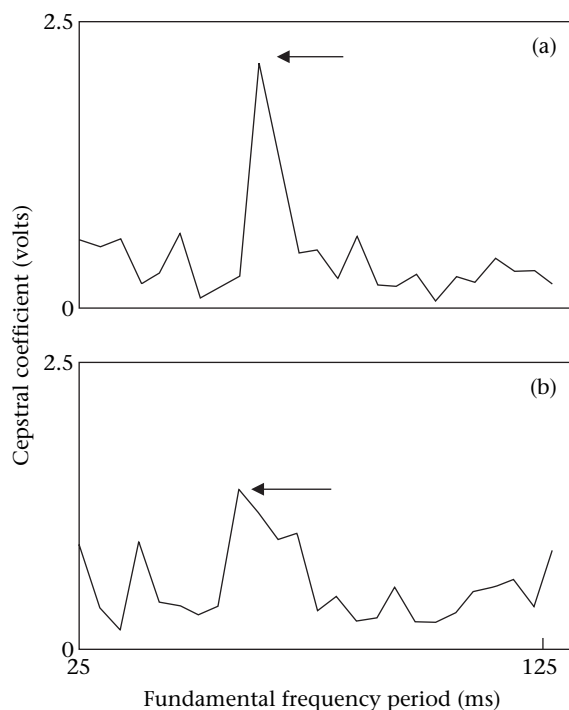


Figure 3. Exemplar of a cepstrum with a high peak (a) and with a low peak (b) (measure 16 in Table 1). The cepstral coefficient is the value in volts, indicated by the arrows, at the peak corresponding to the fundamental frequency in milliseconds (see Methods). Harmonic signals with high tonality and stable pitch result in narrower, higher cepstral peaks, as shown in (a).

features. The cepstral peak coefficient was used to measure periodicity (i.e. tonality) and stability of the pitch period (i.e. short-term changes in focal fold frequency, or 'jitter') in the voice (CEP command in SIGNAL, version 3.1; Engineering Design). The cepstral peak corresponds to the harmonic interval of the spectrum in milliseconds. For example, a power spectrum with a fundamental frequency of 20 Hz and upper harmonics every 20 Hz results in a cepstral peak at 50 ms ($1/\text{harmonic interval} = 1/20 \text{ cycles/s} = 50 \text{ ms}$). The power spectrum of a highly periodic signal (high tonality) with stable pitch (low jitter) will exhibit well-defined harmonics with high peaks and low valleys (as in Fig. 2a), resulting in a cepstrum with a high peak (as in Fig. 3a). Less periodic signals and increased jitter result in power spectra with less clearly defined harmonics and correspondingly lower cepstral peaks (as in Fig. 3b; also see Hillenbrand et al. 1994; Blankenship 2002; Heman-Ackah et al. 2003). In addition, the number of harmonics and their consistency over time positively affect the height of the cepstral peak. In humans, direct measures of jitter are often associated with negative affect (e.g. Rendall 2003), and low cepstral peaks are associated with pathology and dysphonia in the voice (Wolfe & Martin 1997; Heman-Ackah et al. 2003).

When classifying rumble vocalizations according to individual identity and reproductive phase, we had no strong a priori predictions about which acoustic measures would be most salient, so we included all 16 measures in our analyses. In the case of negative emotional arousal, however, we chose several source measures that we

thought may be related to emotional arousal due to physiological mechanisms (see Introduction). We predicted that emotional arousal would result in lower cepstral coefficients (low tonality and high jitter), and higher mean and maximum fundamental frequencies.

Our target was to measure 50 calls for each female but this was only possible for four females due to the poor quality of most calls (signal-to-noise ratio). For the two additional females, we were able to obtain full measurements on 35 calls each, for a total of 270 calls over six females.

Endocrine Data Collection and Analysis

Blood samples were assayed for progesterone (P) and luteinizing hormone (LH) to determine phases of the cycle for three cycling females, following Soltis et al. (2005) and Leong et al. (2003b). Briefly, blood samples were collected twice per week during the luteal phase and daily during the follicular period. Serum P and LH concentrations were quantified using enzyme-immunoassays (EIA). Intra- and interassay coefficients of variation were 7.5% and 11.2%, respectively, for the progesterone EIA, and 8.7% and 13.6% for the LH EIA.

The patterns of serum P and LH concentrations were used to determine the different phases of the oestrous cycles, including two waves of follicular growth: the luteal, anovulatory follicular and ovulatory follicular phases. There were three cycling and three noncycling females. Previous research showed that females increase their rate of rumble production during the anovulatory follicular phase and it was proposed that this increase might function to attract males over long distances (Leong et al. 2003b). Therefore, we examined rumbles produced during the anovulatory follicular phase for acoustic distinctiveness.

Behavioural Data Collection and Analysis

Three to four observers documented behaviour for each 1-h observation session using Panasonic mini-digital video cameras, following Soltis et al. (2005) and Leong et al. (2003b). Briefly, field observers filmed elephants from viewing locations surrounding the enclosure for 10-min focal periods. On average, two 10-min periods were recorded per 1-h observation per elephant. The video signals from all four field video cameras were routed through an analogue quad-splitter and copied to a VHS tape with four windows, each containing the signal from one of the mini-digital video cameras, synchronized in time, with the accompanying audio information from radio transmissions.

Quad-split videotapes were analysed to place rumble vocalization behaviour into social context. For each measurable vocalization, we noted the proximity of the caller to other group members and their relative dominance ranks. Animals were considered in proximity if they were within 8 m, and dominance ranks were determined by displacements (see Soltis et al. 2005). In this way, we were able to compare the acoustic structure of rumbles produced in different social contexts.

Table 1. Acoustic measures

Measures		Definition
1	Start frequency	Fundamental frequency at onset of the signal (Hz)
2	Maximum frequency	Maximum frequency of the fundamental across the signal (Hz)
3	Minimum frequency	Minimum frequency of the fundamental across the signal (Hz)
4	End frequency	Fundamental frequency at the end of the signal (Hz)
5	Duration	Length of signal (ms)
6	% Maximum	Length (in ms) from signal onset to maximum frequency/duration
7	Range	Maximum frequency–minimum frequency
8	Curve	Range/duration
9	Mean frequency	Mean fundamental frequency across the signal weighted by amplitude (Hz)
10	Formant frequency 1	Centroid value of the first formant measured for 100 ms from the midpoint of the signal (Hz)
11	Formant frequency 2	Centroid value of second formant (Hz)
12	Formant frequency 3	Centroid value of third formant (Hz)
13	Relative amplitude of first formant	Amplitude of first formant (dB-volts)/mean amplitude of first three formants (dB-volts)
14	Relative amplitude of second formant	Amplitude of second formant (dB-volts)/mean amplitude of first three formants (dB-volts)
15	Relative amplitude of third formant	Amplitude of third formant (dB-volts)/mean amplitude of first three formants (dB-volts)
16	Cepstral coefficient	Value of peak at the fundamental period of a real cepstrum for the middle 2 s of the signal (volts). (Note that ‘rev’ vocalizations are less than 1 s, so for these calls, the measure was on a 512-point sample at call midpoint.)

Statistical Analyses

We used multidimensional scaling analysis to examine the pattern of acoustic variation in rumbles. Specifically, we wanted to determine whether rumbles fall into acoustically distinct subtypes without stipulating a priori categories. For comparison, we also took the same 16 measures on ‘rev’ vocalizations. The rev is a rare vocalization (17 in the data set, of which 10 were measurable), but is closest in acoustic structure to the rumble compared to any other elephant vocalization (Leong et al. 2003a). Like the rumble, the rev is a frequency-modulated, harmonically rich signal, but it differs in qualitative ways. For example, the range of mean fundamental frequencies across revs is 59.7–83.4 Hz ($N = 10$), while the range for rumbles is 11.2–26.0 Hz ($N = 270$). Similarly, the range in duration across revs is 427–907 ms, while the range for rumbles is 1956–10411 ms. By comparing the difference between these two obviously distinct calls with the differences found within rumbles, judgment can be made as to whether or not there are different rumble subtypes from a strictly structural standpoint.

Predictive discriminant function analysis (DFA) was used to determine whether rumbles could be categorized according to a priori categories, namely, individual identity and reproductive phase of the cycle. We tested validation of the classifications in one of two ways. When sample size allowed (individual identity analysis), we withheld 25% of calls from each female, and reclassified those on the basis of the functions originally derived from the selected calls. When sample size was small (reproductive phase analysis), we performed a leave-one-out classification, in which we reclassified each case according to the functions derived from all cases other than that case. Both of these methods are conservative tests of the predictive ability of the classification to accurately classify

calls of unknown category (Quinn & Keough 2002). MANOVA was used to test for statistically significant differences between categories.

We confirmed that the assumptions of DFA/MANOVA were met (Quinn & Keough 2002). First, we checked individual variables for normality and outliers by visually inspecting histograms. Variables showed approximate normal distributions, but for many variables, outliers were present. Therefore, the data were log transformed before DFA and MANOVA. Homogeneity of variance across groups was examined by visual inspection of scatterplots in discriminant space. The difference in spread across groups was modest (lowest spread was 2/3 that of the highest spread). In the analysis of reproductive state, however, the difference in sample size was large ($N_1 = 20$, $N_2 = 111$), which can exacerbate deviations from homogeneity of variance. We used Pillai’s trace statistic, which is the most robust to such deviations, but the MANOVA on reproductive state will nevertheless be interpreted with caution.

Finally, we used the Wilcoxon signed-ranks test to examine three variables that we predicted would be related to emotional state, the mean and maximum frequency of the fundamental and the cepstral coefficient. All tests were performed in SPSS (version 11.0, SPSS, Chicago, Illinois, U.S.A.), except for the Wilcoxon signed-ranks tests, which were hand-calculated according to Siegel (1956). Two-tailed alpha was set at 0.05.

RESULTS

Are There Acoustically Distinct Subcategories of Rumbles?

We used multidimensional scaling (MDS) techniques to determine whether rumbles can be classified into subtypes

based on 16 acoustic measures (Table 1). The first 15 rumbles from each of six females were entered into the analysis ($N = 90$). For comparison, the same measures were taken on 10 'rev' vocalizations, the vocalization closest to the rumble in acoustic structure (Leong et al. 2003a). There was clear acoustic separation between rumbles and revs (Fig. 4). Although there was extensive acoustic variation among rumbles, they did not fall into distinct clusters or subtypes.

Interpretation of MDS results is essentially subjective, but a measure of the validity of the scatterplot is a strong relationship between actual dissimilarity measures between vocalizations and the observed distances in the MDS scatterplot (Quinn & Keough 2002). High stress values (above 0.3) indicate that the scatterplot distances are arbitrary with respect to the actual distances, and low stress values (less than 0.1) are considered ideal. Kruskal's stress test yielded a value of 0.10895, indicating that the scatterplot in Fig. 4 accurately reflected acoustic distance based on the 16 input measurements. Also, the MDS model accounted for a high proportion of the variance in the dissimilarity matrix ($R^2 = 0.97905$).

MDS in SPSS only allowed for 100 cases in a single analysis, so the number of rumbles in the analysis was limited to 90, even though the total number of measured rumbles in the data set was 270. In Fig. 4, the first 15 rumbles from each female ($N = 6$) are shown. Analysis of the last 15 rumbles for each female, and a random 15 rumbles from each female, produced similar results.

Individual Identity and Acoustic Variation of Rumbles

We performed a discriminant function analysis (DFA) on 270 rumbles ($N = 6$ females) to examine the extent to which individual identity may be encoded in rumble vocalizations. The sample was split by randomly withholding 25% of the calls from each female ($N = 70$), for later use in validation, and entering the remaining 200

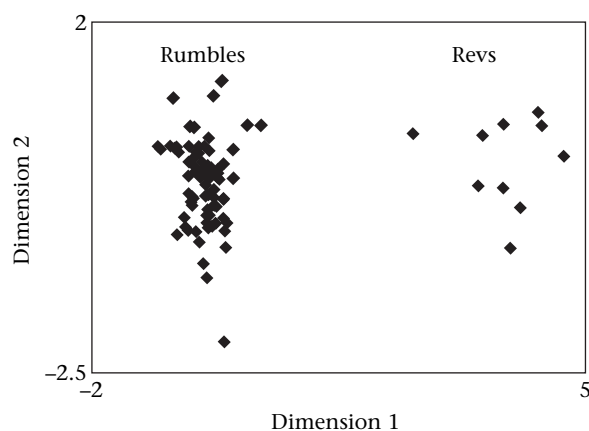


Figure 4. Results of a multidimensional scaling analysis. Ten 'rev' vocalizations and 90 'rumble' vocalizations are shown in multidimensional space based on 16 acoustic measures (Table 1). Revs are clearly separated from rumbles, but rumbles do not fall into distinct clusters or subtypes.

vocalizations into the original analysis. In univariate analyses, all variables differed significantly among individuals (all $P < 0.01$). In the multivariate DFA, the first two factors explained 90.3% of the variance, and MANOVA showed a significant difference among individuals (Pillai's trace = 1.390, $F_{70,1275} = 7.011$, $P < 0.001$). Table 2 shows the variance explained by each of the five functions, and the variable loadings on each function. Formant frequencies separated individuals on the first function, and features related to the fundamental contour separated individuals on the second function. In the split-sample validation, the 70 withheld rumbles were classified according to individual identity with a 60.0% (42/70) success rate, compared to the chance expectation of 16.7%. There was extensive variation in classification success rate across individuals, however, ranging from 22.2 to 100% correct.

Reproductive State and Acoustic Variation of Rumbles

We used DFA to examine differences in rumbles ($N = 131$) across the reproductive phases of three cycling females (luteal, anovulatory follicular and ovulatory follicular phases; see Methods). MANOVA did not show a significant difference in rumbles when comparing all three phases of the cycle (Pillai's trace = 0.337, $F_{32,228} = 1.446$, $P = 0.066$). Next, we compared rumbles during the anovulatory follicular phase, which occurs several weeks prior to ovulation when rumble production is known to increase (Leong et al. 2003b), to those rumbles occurring during the other two phases of the cycle. Only 20 rumbles fell into the anovulatory follicular phase, so we used leave-one-out cross validation rather than the split-sample validation method. Table 3 shows the results of univariate analyses for each variable and the structure matrix for the multivariate DFA. In the DFA, the first (and only) function explained 100% of the variance, and MANOVA showed a significant difference between the two categories of rumble (Pillai's trace = 0.216, $F_{16,114} = 1.965$, $P = 0.021$). The first formant frequency was strongly correlated with the first function (>0.6), the mean and end frequencies showed intermediate correlations (>0.4), and all other variables showed weak correlations. In the leave-one-out cross validation, 84.0% of cases were correctly classified according to reproductive phase, compared to the expectation of 50.0%. However, most of the calls in the anovulatory follicular phase were incorrectly classified (only 3/20 = 15% correctly classified); the success rate for classifying calls of other phases combined was high (107/111 = 96.4% correctly classified).

Emotional State and Acoustic Variation of Rumbles

We examined several measures thought to be associated with emotional arousal based on the social context of their production. Of the 270 measurable rumbles, all six females were housed in the main enclosure and the caller

Table 2. Variance explained, and structure matrix for discriminant function analysis on individual identity

	Functions				
	1	2	3	4	5
Variance explained (%)	75.3	14.9	5.6	2.4	1.8
Cumulative variance (%)	75.3	90.3	95.8	98.2	100.0
Variables					
Formant frequency 1	0.776	−0.118	0.007	−0.265	−0.065
Formant frequency 3	− 0.385	−0.187	−0.076	0.096	−0.111
% Maximum	0.278	−0.058	0.167	0.196	0.140
Minimum frequency	−0.027	− 0.741	0.015	−0.238	0.417
Start frequency	−0.063	− 0.723	0.014	−0.086	0.104
End frequency	0.009	− 0.547	0.204	−0.418	0.334
Mean frequency	0.120	− 0.491	0.458	−0.071	0.160
Maximum frequency	0.170	− 0.470	0.359	−0.255	0.032
Formant frequency 2	−0.141	0.416	0.131	0.171	0.300
Curve	0.156	−0.097	0.381	−0.230	−0.250
Duration	0.136	0.108	− 0.360	0.163	0.105
Relative amplitude of first formant	0.094	−0.215	0.336	−0.159	0.237
Relative amplitude of second formant	−0.183	−0.040	0.169	0.365	−0.042
Relative amplitude of third formant	−0.186	−0.173	0.057	0.343	−0.340
Cepstral coefficient	0.132	0.135	−0.139	−0.058	0.266
Range	0.165	−0.037	0.126	−0.090	− 0.250

Factor on which each variable loaded the strongest is shown in bold.

was visible on screen in 75 cases. For these cases, we defined ‘tense’ social contexts as those in which the caller was in proximity to a dominant animal (within 8 m), and ‘calm’ social contexts as those in which the caller was not in proximity to dominant animals. Tense social situations were not associated with an increase in fundamental frequency measures (maximum frequency: Wilcoxon signed-ranks test: $T = 8$, $N = 6$ females, NS; mean frequency: $T = 7$, $N = 6$ females, NS). Emotional state was associated with cepstral coefficient values, however. Tense

social situations were characterized by lower mean cepstral values in all six females, indicating lower tonality and a less stable pitch period in the voice ($T = 0$, $N = 6$ females, $P < 0.05$; Fig. 5).

DISCUSSION

How Many Rumble Subtypes Are There?

The analysis presented here showed that the rumble vocalizations of captive African elephants could not be subdivided into acoustically distinct subtypes, but that extensive graded variation existed across rumbles. This result, generated from a small captive group, may not

Table 3. Structure matrix from discriminant function analysis and results from univariate analyses on reproductive phase of the cycle

Measure	Function 1	$F_{1,129}$	P
Formant frequency 1	−0.617	13.538	0.000
Minimum frequency	−0.471	7.883	0.006
End frequency	−0.437	6.802	0.010
Relative amplitude of first formant	−0.364	4.720	0.032
Mean frequency	−0.347	4.292	0.040
Formant frequency 2	−0.268	2.565	0.112
Maximum frequency	−0.265	2.489	0.117
Relative amplitude of second formant	0.241	2.072	0.152
Cepstral coefficient	−0.221	1.731	0.191
Start frequency	−0.152	0.823	0.366
Duration	−0.121	0.523	0.471
Relative amplitude of third formant	0.099	0.347	0.557
Formant frequency 3	−0.084	0.253	0.610
Range	0.077	0.213	0.645
% Maximum	0.053	0.100	0.752
Curve	0.006	0.001	0.970

Function 1 shows loadings of each variable on the first and only function in the discriminant function analysis. F and P values are shown for the univariate analyses.

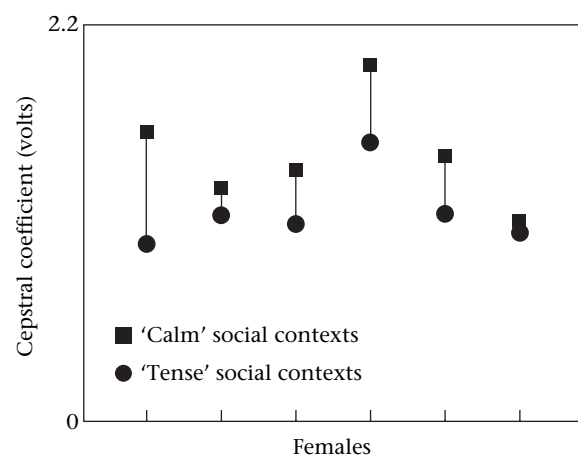


Figure 5. Mean cepstral coefficient and emotional arousal in African elephants. For each female, mean cepstral coefficient of rumbles produced in ‘tense’ and ‘calm’ social contexts are shown (see text for definitions).

generalize to the species as a whole, however. First, social and ecological experiences of this group of captive elephants are limited compared to the natural experiences of wild elephants, thus limiting the contexts in which naturally occurring rumbles will be produced. Wild elephants may indeed use acoustically distinct rumble subtypes in contexts that do not exist in captivity. Second, the analyses presented here were based on the same captive group of animals used in the classification by Leong et al. (2003a). In contrast to the results presented here, the previous analysis distinguished three acoustic rumble types based on visual inspection of spectrograms. There were acoustically distinct outliers in the rumble analysis presented here (see Fig. 4), and most of the upper outliers were labelled as 'noisy rumbles' in the previous visual inspection classification (Leong et al. 2003a). These outlier rumbles were characterized by unusually high frequencies across the fundamental contour and, with a larger sample, may be shown to constitute an acoustic subtype, which itself may be similar to the 'roar' vocalization described by Berg (1983). In short, no acoustically distinct subtypes could be found in this data set, but similar work on larger numbers of wild elephants will be required to determine whether rumble variation is best described as discrete or graded.

Contact Rumbles

One commonly proposed function of the African elephant rumble is a long-distance contact call among females. The social core of elephant society is the family unit, which consists of related adult females and their immature offspring, and multiple families form larger, fission–fusion social units sometimes referred to as bond groups or clans (Laws et al. 1975; Moss & Poole 1983; Poole et al. 1988; McComb et al. 2000). When related females are out of contact, they may localize one another in space and coordinate movements using rumbles as long-distance contact calls (Poole et al. 1988; Langbauer et al. 1991; McComb et al. 2003). In a companion paper, we also showed that affiliated females in a captive group exchange rumbles in antiphonal sequences, sometimes when out of close contact (Soltis et al. 2005). These results suggest that individuals may be able to recognize one another by their voice alone, as evidence suggests is the case in many other animal species (e.g. Rendall et al. 1986; Aubin et al. 2000; Charrier et al. 2002; Soltis et al. 2002). The results presented here, showing that female elephant rumbles are individually distinctive, are consistent with this view. Additionally, Clemins et al. (2005) used human speech recognition techniques to successfully classify Disney Animal Kingdom elephant vocalizations by individual identity. These results for captive elephants echo those of McComb et al. (2003), who used a stepwise discriminant function analysis to acoustically separate 99 rumbles from 13 wild female African elephants, also using source and filter features.

Our DFA results suggests that both source and filter features contributed to individual variation (Table 2). Formant frequencies loaded strongest on the first factor,

suggesting that vocal tract filter effects are important. Formant structure is also known to differ among individuals in primates (e.g. Rendall et al. 1998). McComb et al. (2003) estimated African elephant vocal tract length based on rumble interformant distance (see Fitch 1997), suggesting a functional vocal tract length of 2.8 m during rumble production, which implicates the trunk in addition to the oral cavity in elephant rumble production. Using the same calculations, but inserting our mean inter-formant distance of 56.0 Hz ($N = 270$ rumbles), results in a similar functional vocal tract length of 2.95 m, corroborating the implication of the trunk in rumble production. Source features are also important in separating individual African elephant rumbles, however. One source feature loaded strongest on the first function and many loaded on the second function, including measures of absolute fundamental frequency and frequency contour (Table 2).

Mate Attraction Rumbles

Another commonly proposed function of the female rumble is a long-distance mate attraction call (Langbauer et al. 1991; Poole 1999; Leong et al. 2003b). Adult males are mainly solitary, but sometimes live in all-male herds, and they associate with females for the most part only when mating (e.g. Moss & Poole 1983). Males in musth, a behavioural and physiological state of reproductive readiness (Poole 1987), respond to playbacks of female rumbles by approaching the sound source, whereas non-musth males do not (Poole 1999). Furthermore, in a captive study, Leong et al. (2003b) showed that females increased their rumbles during the anovulatory follicular phase 3–6 weeks before ovulation. Since males are distributed widely in space, signalling or detecting impending ovulation may be more adaptive than signalling or detecting current ovulation. According to this model, males monitor their auditory environment with regard to female vocal activity, perhaps attending to specific acoustic properties that may be associated with impending ovulation, and use olfactory and visual cues to female reproductive state when in closer contact (Rasmussen & Schulte 1998; Langbauer 2000; Leong et al. 2003b). The preliminary data presented here suggesting that anovulatory follicular rumbles are acoustically distinctive is consistent with this view. Using automated human speech recognition techniques, Clemins et al. (2005) also successfully classified rumbles from Disney's Animal Kingdom elephants according to reproductive phase of the cycle. However, only three cycling females contributed to these results, and in the present analysis, some assumptions required for statistical tests were not met and the classification of uncategorized calls was only modestly successful, so these results need to be replicated.

Emotional Arousal in Rumbles

In humans and other primates, nonspecific emotional arousal influences the acoustic quality of the voice through physiological mechanisms (see Introduction).

We examined three source features: mean fundamental frequency, maximum fundamental frequency and the cepstral coefficient (Table 1). The fundamental frequency measures were not related to emotional arousal, but elephant rumbles produced in the presence of dominant animals had lower cepstral coefficients than those produced outside of the presence of dominant animals. Cepstral coefficients conflate several acoustic parameters in the voice (e.g. tonality and jitter; see *Methods*), so it is unclear to what extent each parameter contributed to the values obtained here. Further work will be needed to elucidate the specific acoustic parameters that reflect affect in African elephants. Different vocalization types have been associated with emotional arousal in African elephants (for review see *Langbauer 2000*) as well as other mammals (e.g. *Schon et al. 2001; Jovanovic & Gouzoules 2001*). *Berg (1983)* reported that captive African elephants produce high-frequency vocalizations (mainly trumpets) during periods of emotional arousal, usually related to aggression or mating, and that they produce low-frequency vocalizations (mainly rumbles, or 'growls' in *Berg's* terminology) during more relaxed social contexts. *Berg* also noted that recipients of intraspecific aggression sometimes produce 'cries' and 'growls' (again, growls = rumbles), indicating that recipients of aggression sometimes produce rumbles. The results presented here, however, provide the first evidence that emotional arousal may be reflected in the acoustic details of rumbles.

Rumbles reflecting affect during dominance interactions may serve communicative functions. Such voice characteristics may be originally related solely to affect, but such acoustic characteristics may contribute to communicative systems over evolutionary time. For example, if negative affect in the voice during close social interactions was regularly associated with an unwillingness to engage in physical combat, members of the species may have evolved to recognize such calls as indicators of submission. At this stage, signals may become decoupled from inner state and the structure may further evolve based on its effect on receiver behaviour (*Bachorowski & Owren 2003*). Such submissive signals could presumably benefit both signallers and receivers by avoiding the costs of unnecessary fighting when relative dominance status is not being actively contested (*van Rhijn & Vodegel 1980*), and such signals of submission have been demonstrated empirically (e.g. Atlantic salmon, *Salmo salar*: *O'Connor et al. 1999*). A nonexclusive alternative explanation is that such negative affect in the voice alerts potential allies during contests with unaffiliated conspecifics.

These findings point the way for further study. First, these results and those from previous studies strongly suggest that elephants can recognize specific individuals by their voice alone, but playback experiments will be needed to demonstrate this unequivocally. Second, as stated above, the existence of an acoustically distinctive call by females that attracts males needs to be further examined. Third, there is a multitude of measures of affect in the voice in addition to those few examined here. Source-filter theory predicts that physiological mechanisms related to emotional arousal could affect voice characteristics at several points along the vocal production

pathway, including respiration, vocal fold enervation and shape of the vocal tract (*Fitch & Hauser 1995; Bachorowski 1999*). Fourth, we provided evidence that the structural variability of rumbles is graded in this group, but calls could nevertheless be perceived in a categorical manner. Investigation into auditory perception of the African elephant would also be useful. Lastly, we have emphasized the internal structure of rumbles, but sequences of calls may also serve communicative functions in African elephants.

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References

- Aubin, T., Jouventin, P. & Hildebrand, C. 2000. Penguins use the two-voice system to recognize each other. *Proceedings of the Royal Society of London, Series B*, **267**, 1081–1087.
- Bachorowski, J. 1999. Vocal expression and perception of emotion. *Current Directions in Psychological Science*, **8**, 53–57.
- Bachorowski, J. & Owren, M. J. 1995. Vocal expression of emotion: acoustic properties of speech are associated with emotional intensity and context. *Psychological Science*, **6**, 219–224.
- Bachorowski, J. & Owren, M. J. 1999. Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech. *Journal of the Acoustical Society of America*, **106**, 1054–1063.
- Bachorowski, J. & Owren, M. J. 2003. Sounds of emotion: production and perception of affect-related vocal acoustics. *Annals of the New York Academy of Science*, **1000**, 244–265.
- Bayart, F., Hayashi, K. T., Faull, K. F., Barchas, J. D. & Levine, S. 1990. Influence of maternal proximity on behavioral and physiological responses to separation in infant rhesus monkeys. *Behavioral Neuroscience*, **104**, 98–107.
- Berg, J. K. 1983. Vocalizations and associated behaviors of the African elephant (*Loxodonta africana*) in captivity. *Zeitschrift für Tierpsychologie*, **63**, 63–79.
- Blankenship, B. 2002. The timing of nonmodal phonation in vowels. *Journal of Phonetics*, **30**, 163–191.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Catchpole, C. K. & Slater, P. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Charrier, I., Mathevon, N. & Jouventin, P. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, **205**, 603–612.
- Clemins, P. J., Johnson, M. T., Leong, K. M. & Savage, A. 2005. Automatic classification and speaker identification of African elephant (*Loxodonta africana*) vocalizations. *Journal of the Acoustical Society of America*, **117**, 956–963.

- Emerson, S. B. & Boyd, S. K. 1999. Mating vocalizations of female frogs: control and evolutionary mechanisms. *Brain, Behavior and Evolution*, **53**, 187–197.
- Fichtel, C., Hammerschidt, K. & Jurgens, U. W. E. 2001. On the vocal expression of emotion, a multi-parametric analysis of different states of aversion in the squirrel monkey. *Behaviour*, **138**, 97–116.
- Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**, 1213–1222.
- Fitch, W. T. & Hauser, M. D. 1995. Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on “honest” advertisement. *American Journal of Primatology*, **37**, 191–219.
- Green, S. 1975. Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In: *Primate Behavior: Developments in Field and Laboratory Research*. Vol. 4 (Ed. by L. A. Rosenblum), pp. 1–102. New York: Academic Press.
- Hauser, M. D. 2000. A primate dictionary? Decoding the function and meaning of another species’ vocalizations. *Cognitive Science*, **24**, 445–475.
- Heman-Ackah, Y. D., Heuer, R. J., Michael, D. D., Ostrowski, R., Horman, M., Baroody, M. M., Hillenbrand, J. & Sataloff, R. T. 2003. Cepstral peak prominence: a more reliable measure of dysphonia. *Annals of Otology Rhinology and Laryngology*, **112**, 324–333.
- Hillenbrand, J., Cleveland, R. A. & Erickson, R. L. 1994. Acoustic correlates of breathy vocal quality. *Journal of Speech and Hearing Research*, **37**, 769–778.
- Janik, V. M. 1999. Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. *Animal Behaviour*, **57**, 133–143.
- Jovanovic, T. & Gouzoules, H. 2001. Effects of nonmaternal restraint on the vocalizations of infant rhesus macaques (*Macaca fuscata*). *American Journal of Primatology*, **53**, 33–45.
- Langbauer, W. R. 2000. Elephant communication. *Zoo Biology*, **19**, 425–445.
- Langbauer, W. R., Payne, K. B., Charif, R. A., Rapaport, L. & Osborn, F. 1991. African elephants respond to distant playbacks of low-frequency conspecific calls. *Journal of Experimental Biology*, **157**, 35–46.
- Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. 1975. *Elephants and Their Habitats: the Ecology of Elephants in North Bunyoro, Uganda*. Oxford: Clarendon.
- Leong, K. M., Ortolani, A., Burks, K. D., Mellen, J. D. & Savage, A. 2003a. Quantifying acoustic and temporal characteristics of vocalizations for a group of captive African elephants *Loxodonta africana*. *Bioacoustics*, **13**, 213–231.
- Leong, K. M., Ortolani, A., Graham, L. H. & Savage, A. 2003b. The use of low-frequency vocalizations in African elephant (*Loxodonta africana*) reproductive strategies. *Hormones and Behavior*, **43**, 433–443.
- McComb, K., Moss, C., Sayialel, S. & Baker, L. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour*, **59**, 1103–1109.
- McComb, K., Reby, D., Baker, L., Moss, C. & Sayialel, S. 2003. Long-distance communication and acoustic cues to social identity in African elephants. *Animal Behaviour*, **65**, 317–329.
- McCowan, B. & Reiss, D. 2001. The fallacy of ‘signature whistles’ in bottlenose dolphins: a comparative perspective of ‘signature information’ in animal vocalizations. *Animal Behaviour*, **62**, 1151–1162.
- Moss, C. J. & Poole, J. H. 1983. Relationships and social structure of African elephants. In: *Primate Relationships: an Integrated Approach* (Ed. by R. A. Hinde), pp. 315–325. Oxford: Blackwell Scientific.
- Nowicki, S. & Nelson, D. A. 1990. Defining natural categories in acoustic signals: comparison of three methods applied to ‘chick-a-dee’ call notes. *Ethology*, **86**, 89–101.
- O’Connor, K. I., Metcalfe, N. B. & Taylor, A. C. 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour*, **58**, 1269–1276.
- Poole, J. H. 1987. Rutting behavior in African elephants: the phenomenon of musth. *Behaviour*, **102**, 283–316.
- Poole, J. H. 1999. Signal assessment in African elephants: evidence from playback experiments. *Animal Behaviour*, **58**, 185–193.
- Poole, J. H., Payne, K., Langbauer, W. R. & Moss, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, **22**, 385–392.
- Porges, S. W. 1995. Cardiac vagal tone: a physiological index of stress. *Neuroscience and Biobehavioral Reviews*, **19**, 225–233.
- Price, J. J. 1999. Recognition of family-specific calls in stripe-backed wrens. *Animal Behaviour*, **57**, 483–492.
- Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.
- Rasmussen, L. E. L. & Schulte, B. A. 1998. Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. *Animal Reproduction Science*, **53**, 19–34.
- Rendall, D. 2003. Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *Journal of the Acoustical Society of America*, **113**, 3390–3402.
- Rendall, D., Rodman, P. S. & Emond, R. E. 1986. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.
- Rendall, D., Owren, M. J. & Rodman, P. S. 1998. The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations. *Journal of the Acoustical Society of America*, **103**, 602–614.
- van Rhijn, J. G. & Vodegel, R. 1980. Being honest about one’s intentions. An evolutionary stable strategy for animal conflicts. *Journal of Theoretical Biology*, **85**, 623–641.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D. & Irvine, A. B. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour*, **57**, 41–50.
- Scherer, K. R. 1986. Vocal affect expression: a review and a model for future research. *Psychological Bulletin*, **99**, 143–165.
- Schon, P. C., Puppe, B. & Manteuffel, G. 2001. Linear predictive coding analysis and self-organizing feature map as tools to classify stress calls of domestic pigs (*Sus scrofa*). *Journal of the Acoustical Society of America*, **110**, 1425–1431.
- Semple, S. & McComb, K. 2000. Perception of female reproductive state from cues in a mammal species. *Proceedings of the Royal Society of London, Series B*, **267**, 707–712.
- Semple, S., McComb, K., Alberts, S. & Altmann, J. 2002. Information content of female copulation calls in yellow baboons. *American Journal of Primatology*, **56**, 43–56.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Soltis, J. 2004. The signal functions of early infant crying. *Behavioral and Brain Sciences*, **27**, 443–490.
- Soltis, J., Bernhards, D., Donkin, H. & Newman, J. D. 2002. The squirrel monkey chuck call: vocal response to playback chucks based on acoustic structure and affiliative relationship with the caller. *American Journal of Primatology*, **57**, 119–130.
- Soltis, J., Leong, K. & Savage, A. 2005. African elephant vocal communication I: antiphonal calling behaviour among affiliated females. *Animal Behaviour*, **70**, 579–589.

- Tobias, M. L., Viswanathan, S. S. & Kelley, D. B. 1998. Rapping, a female receptive call, initiates male–male duets in the South African clawed frog. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 1870–1875.
- Watwood, S. L., Tyack, P. L. & Wells, R. S. 2004. Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, **55**, 531–543.
- Wolfe, V. & Martin, D. 1997. Acoustic correlates of dysphonia: type and severity. *Journal of Communication Disorders*, **30**, 403–416.
- Wycherley, J., Doran, S. & Beebee, T. J. C. 2002. Male advertisement call characters as phylogeographical indicators in European water frogs. *Biological Journal of the Linnean Society*, **77**, 355–365.