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CLASSIFICATION OF AFRICAN ELEPHANT *LOXODONTA AFRICANA* RUMBLES USING ACOUSTIC PARAMETERS AND CLUSTER ANALYSIS

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ABSTRACT

It has been suggested that African savanna elephants *Loxodonta africana* produce 31 different call types (Langbauer 2000). Various researchers have described these calls by associating them with specific behavioural contexts. More recently Leong et al. (2003) have attempted to classify elephant call types based on their physical properties. They classified 8 acoustically distinct call types from a population of captive elephants. This study focuses on one of these call types, the rumble, in a wild population of elephants in Kruger National Park, South Africa. A single family group of elephants was followed to record group behaviours and vocalizations from January through August 2001. By measuring the physical properties of 663 rumbles and subjecting these to cluster analysis, we present evidence that shows that rumbles can be categorized by their physical properties and that the resulting rumble types are associated with specific group behaviours. We characterize three types of rumbles that differ significantly by ten acoustic parameters. Two rumble types were associated with the elephant group feeding and resting, while the third was associated with socializing and agitation.

Keywords: African elephant, *Loxodonta africana*, acoustic communication, call categorization, cluster analysis.

INTRODUCTION

An essential component to understanding the acoustic communication of any species is the ability to distinguish between different call types. For a signal to be interpreted correctly by a conspecific, the receiver must be able to make this distinction as well. This distinction is sometimes made easier by sending a complementary signal using another sensory modality. For instance, an acoustic signal might be accompanied by a visual signal that would decrease ambiguity about the meaning of the acoustic signal. The behavioural context in which the signal is given can also give clues as to the meaning of the signal. However, in situations where signals are received in only one modality (such as when one modality operates at greater distances than other modalities), the coding of the signal must be structured such that it can be interpreted (i.e., correctly categorized) by the receiver of that signal. In these single modality signals there must be enough physical structure in the signal to decrease ambiguity in the interpretation of the signal by the receiver. In addition, that coding structure must be maintained over the distance between the sender and the intended receiver.

African elephants produce low frequency vocalizations that they respond to at distances of around 2 kilometres (Langbauer et al. 1991, McComb et al. 2003). It has been suggested that these rumbles are used for communication between family herds over large distances, as well as for communication within family herds (Payne et al. 1986, Poole et al. 1988). Even during communication within family herds, it is likely that complementary signals produced in modalities other than the acoustic modality would not reach all group members, because family groups will spread out considerable distances (sometimes to distances of 400 meters, pers. obs.). Other family group members would however be able to place these acoustic signals within broad behavioural contexts (e.g. group feeding). Other than the acoustic modality, the communication modalities that elephants use (for review see Langbauer 2000), are not reliable over the distances which elephants are reported to communicate. Therefore there should be sufficient coding in their vocalizations for receivers to interpret the meaning of the signal, if indeed there are distinct categories of calls with specific meanings in elephant communication.

Early attempts at categorizing different elephant call types have done so by associating calls to specific behaviours, and giving a brief description of the physical properties of the calls (Berg 1983, Poole et al. 1988). In this way, 31 call types were described (Langbauer 2000). Most recently Leong et al. (2003), in an attempt to standardize the classification of African elephant vocalizations, used the measures of bandwidth, sound quality (i.e. whether the sound is a tonal harmonic, pulsatile, or noisy), fundamental frequency, presence of infrasonic components, and duration to classify calls. Based on these physical properties they defined 8 mutually exclusive call types, 3 of which were rumble variants (Noisy Rumble, Loud Rumble, and Rumble). These 3 rumble types were differentiated by bandwidth (i.e., the number of higher harmonics present in the call). A cross-correlation analysis was then conducted on the fundamental frequency contour of the Rumble call type, as this was the most common call. This indicated the presence of 5 rumble types, but when subjected to multi-dimensional scaling, there was little clustering between the call types. This suggests either that rumble types grade into each other, or that the fundamental frequency contour is not the physical property of a rumble that is used for coding the meaning of these signals. The aim of this study was to categorize elephant rumbles using not just frequency contours but also other physical parameters of this call type.

METHODS

Forty-two hours of recordings were made between January and August 2001 in the southern part of Kruger National Park (KNP), South Africa using a TASCAM DA-P1 DAT recorder (sampling rate 48 kHz) and a Neumann KM 131 microphone. Recording sessions were conducted on foot or occasionally in a vehicle, and consisted mostly of a focal family unit, although there were many times when other family groups or adult males were in the vicinity as well. Audio notes were made of group behaviour any time this changed (see Results for list of behaviours). Recordings were transferred in the lab from the DAT tape into windows PCM wave files by using the digital out line on the DAT recorder and the digital in line on a VX222 Digigram sound card. Cool Edit Pro V1.2 was used to create these wave files, to down sample the files to 16 kHz (for faster generation of spectrograms since we were only interested in low frequency sound) and for subsequent cueing and filtering. Each rumble was located by listening to the recording and by observing its spectrogram. A start and end cue were marked in the wave file for each rumble, which allowed for the rumbles to be extracted as separate files. Each rumble was then filtered using a Butterworth band pass filter so that only the second harmonic remained. 975 rumbles were identified, 663 of which could be adequately filtered and used in the analysis. The other 312 rumbles were not included in the data set because accurate measurements could not be made due to overlap with other sounds or rumbles.

The second harmonic was extracted because it was consistently the clearest part of the signal in the recordings. In the 10 cases where the second harmonic could not be filtered, either the fundamental or another harmonic was filtered, and any subsequent measures converted to the equivalent of the second harmonic. The contours of the second harmonic and acoustic parameters were extracted using macros developed by McCowan (1995) for Cool Edit pro. The analysis then followed the steps developed by McCowan (1995) and McCowan & Reis (2001). Frequency measures across 60 evenly-spaced points were taken to characterize the frequency contour as well as 19 other parameters (see Table 1). In a number of rumbles, the first 2 frequency measurements returned erroneously high frequencies, and so it was

TABLE 1

List of 19 acoustic parameters and their definitions (adapted from McCowan & Hooper 2002). These acoustic parameters were measured on the contour of the second harmonic of each rumble.

Acoustic Parameter	Description
Coefficient of Frequency Modulation (COFM) (McCowan and Reiss 1995)	Calculated variable that represents the amount and magnitude of frequency modulation across a rumble, computed by summing the absolute values of the difference between sequential frequencies divided by 10000.
Jitter Factor (JF) (Mitani and Brandt 1994)	Calculated variable that represents a weighted measure of the amount of frequency modulation, by calculating the sum of the absolute value of the difference between two sequential frequencies divided by the mean frequency. The sum result is then divided by the total number of points measured minus 1 and the final value is obtained by multiplying it by 100.
Frequency Variability Index (CV) (Mitani and Brandt 1994)	Calculated variable that represents the magnitude of frequency modulation across a rumble, computed by dividing the variance in frequency by the square of the average frequency of a rumble and then multiplying the value by 10.
Inflection Factor (IF)	Percentage of points showing a reversal in slope
Finish Frequency (FF)	Frequency at end of rumble, measured in Hz
Minimum Frequency (MIN)	Lowest frequency attained by rumble, measured in Hz
Peak Frequency (MAX)	Highest frequency attained by rumble, measured in Hz
Mean Frequency (MEAN)	Calculated as average frequency across rumble
Peak Amplitude Frequency (PAF)	Frequency at maximum amplitude
Frequency Range (FR)	Calculated as peak frequency minus minimum frequency
Peak Frequency/Mean Frequency (MAX/MEAN)	Calculated as peak frequency divided by mean frequency

Mean Frequency/Minimum Frequency (MEAN/MIN)	Calculated as mean frequency divided by minimum frequency
Peak Amplitude Location (PAL)	Location of maximum amplitude, given as percentage of duration
Minimum Frequency Location (MINL)	Location of minimum frequency, given as percentage of duration
Peak Frequency Location (MAXL)	Location of peak frequency, given as percentage of duration
Duration (DUR)	Temporal distance of rumble, measured in seconds
Start Slope (SSL)	Calculated as (Frequency 20-Frequency 1)/(Time 20-Time 1)
Middle Slope (MSL)	Calculated as (Frequency 40-Frequency 20)/(Time 40-Time 20)
Final Slope (FSL)	Calculated as (Frequency 60-Frequency 40)/(Time 60-Time 40)

decided not to include the first 2 frequency measures in the analysis. The frequency contour of each rumble was then correlated to every other rumble to obtain a measure of similarity in shape. It is important to point out that this measure is a measure of similarity in shape, not in actual overlap of frequency range. That is to say, if two rumbles have similar frequency modulation (shape), but one starts at 20 Hz and the other at 30 Hz, they will still be highly correlated when using this technique. In essence it is a measure of relative change in frequency, not absolute frequency (McCowan 1995).

In order to cluster the rumbles we then subjected the correlation coefficients (from the frequency contours) to a principal components analysis (PCA) to reduce the number of factors. The resulting factor scores with an eigenvalue greater than 1 were then subjected to cluster analysis. As a separate analysis we also subjected the 19 acoustic parameters to a PCA and then a cluster analysis. In this way we could have a better idea of whether the shape of the call or some other parameter (e.g. duration, max frequency) led to better clustering. The clustering technique used was the MCLUST extension to S-PLUS statistical software (Fraley & Raftery 2002). The advantage of using MCLUST is that one can cluster the data using ten different models and determine which model and number of clusters is most appropriate. As an additional validation of the clustering we randomly selected 75% of the data set and subjected it to MCLUST again. This was repeated 3 times, each time with a new random selection. In addition a linear mixed effects analysis was conducted on each of the 19 acoustic parameters to test which parameters led to the best clustering. A multinominal logistic regression was used to test for associations between the resulting rumble types (clusters) and group behaviour. And finally, a discriminant analysis was conducted to test how well behaviour could be predicted by acoustic parameters. SAS (version 8.0, SAS Institute Inc.), S-Plus (version 6, Insightful Corp.), and Stata (version 7.0 STATA Corp.) were used for the various statistical tests conducted.

RESULTS

Using the default settings for the EMclust command in MCLUST we tested from 1 to 20 clusters and all 10 models. The Bayesian information criterion (BIC) was then used to determine which was the best model and number of clusters. Using the rumble contour data the best model was VEI with 4 clusters (see Figure 1). VEI is a model with a diagonal distribution, variable volume, equal shape, and an orientation that follows the coordinate axes. Fraley and Raftery (2002) label models in MCLUST using the terms Equal, Variable and Identity. The first letter in the model name represents the cluster volume, the

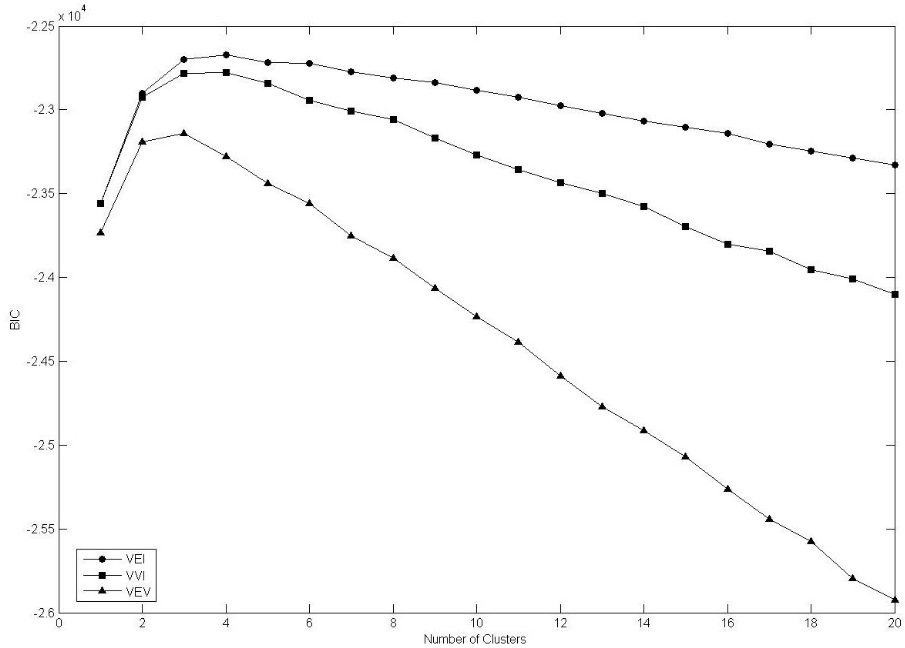

Figure 1. Bayesian information criterion values for 1 to 20 clusters for contour data. The 3 best models are included in this figure. VEI is a model with a diagonal distribution, variable volume, equal shape, and an orientation that follows the coordinate axes. VVI is a model with diagonal distribution, variable volume, variable shape, and an orientation that follows the coordinate axes. VEV is a model with an ellipsoidal distribution, variable volume, equal shape, and variable orientation.

second shape, and the third orientation. The rumble contour data had a mean clustering uncertainty of 0.12 and a median clustering uncertainty of 0.06. Figure 2 shows the distribution of the 4-cluster classification in two-dimensional space. For the acoustic parameter data the best model was VEV with 3 clusters (see Figure 3). VEV is a model with an ellipsoidal distribution, variable volume, equal shape, and variable orientation. The acoustic parameter data had a mean clustering uncertainty of 0.10 and a median clustering uncertainty of 0.04. Figure 4 shows the distribution of the 3-cluster classification in two-dimensional space.

Although both the contour and the acoustic parameter data sets seem to cluster well when used as inputs into MCLUST, the acoustic parameter data set seems to cluster slightly better. The acoustic parameters had a lower overall clustering uncertainty and when one compares the plotted BIC values for the best model in both data sets (Figures 1 and 3), the acoustic parameter data set has a more pronounced peak around the highest BIC values, which one could

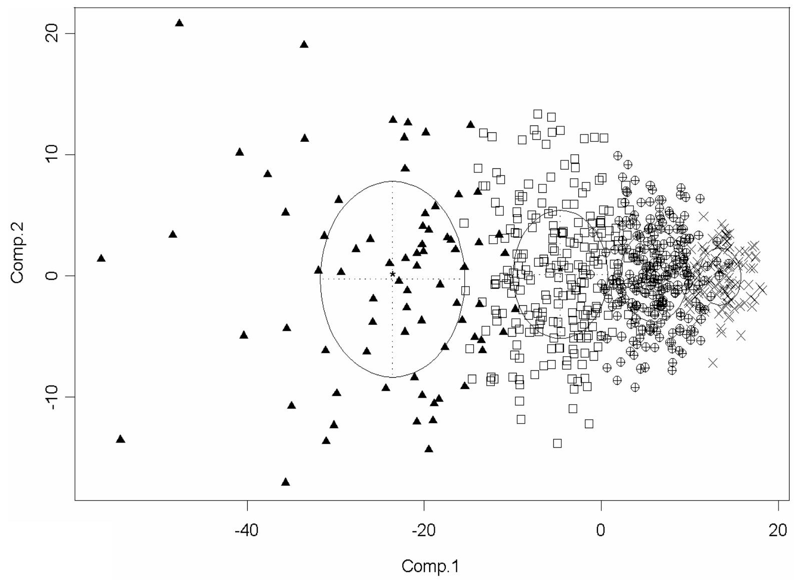

Figure 2. Distribution of the 4 clusters in two-dimensional space for contour data. The ellipsoids show the standard deviations for each cluster.

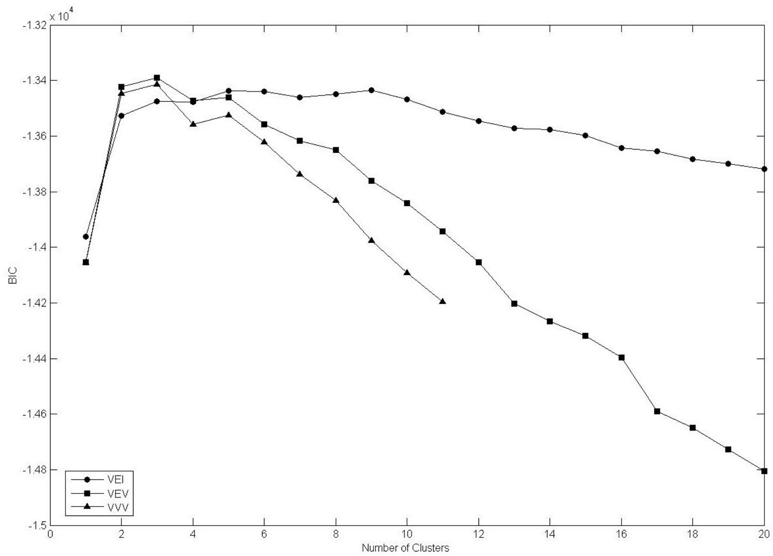

Figure 3. Bayesian information criterion values for 1 to 20 clusters for acoustic parameter data. The 3 best models are included in this figure. VEI is a model with a diagonal distribution, variable volume, equal shape, and an orientation that follows the coordinate axes. VEV is a model with an ellipsoidal distribution, variable volume, equal shape, and variable orientation. VVV is a model with an ellipsoidal distribution, variable volume, variable shape, and variable orientation.

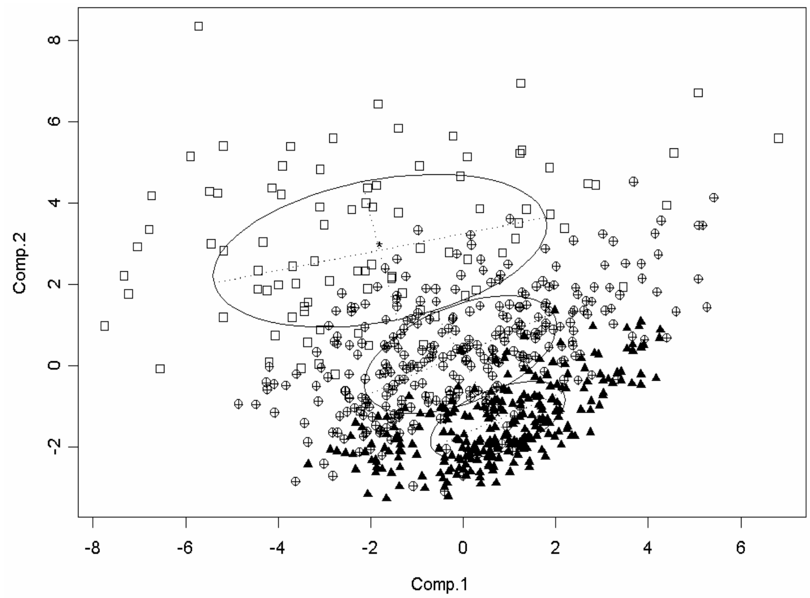

Figure 4. Distribution of the 3 clusters in two-dimensional space for acoustic parameter data. The ellipsoids show the standard deviations for each cluster.

argue indicates a more conclusive number of clusters. Because of this, it was decided to concentrate on the acoustic parameter data set and run MCLUST 3 more times to validate the clustering. Taking a random sub-sample of 75% of the acoustic parameter data we found the following had the highest BIC value; Run 1: VEI-4 clusters, Run 2: VEI-5 clusters, Run 3: VEI-6 clusters (see Table 2). While none of these runs resulted in a cluster of 3 rumble types as having the highest BIC value, 3 clusters did end up in the top 3 BIC values in all 3 runs.

TABLE 2

Results of the highest 3 Bayesian information criterion values for 3 runs of cluster analysis using a random sub-sample of 75% of acoustic parameter data.

Run Number	Number of Clusters	Model	BIC value
1	4	VEI	-10045
	2	VEV	-10046
	3	VEI	-10060
2	5	VEI	-10138
	4	VEI	-10152
	3	VEI	-10159
3	6	VEI	-10043
	3	VEV	-10057
	4	VEI	-10058

TABLE 3

Results of linear mixed effects model for 14 of the 19 acoustic parameters showing significant differences in the 3 rumble types for 13 of the 14 parameters.

Parameter	Summary Statistic	P value
FF	$F_{2,655}$=152.38	<0.0001
MIN	$F_{2,652}$=108.87	<0.0001
MAX	$F_{2,654}$=391.27	<0.0001
MEAN	$F_{2,653}$=226.61	<0.0001
PAF	$F_{2,656}$=135.83	<0.0001
FR	$F_{2,654}$=284.69	<0.0001
MAX/MEAN	$F_{2,653}$=38.79	<0.0001
MEAN/MIN	$F_{2,640}$=18.69	<0.0001
DUR	$F_{2,655}$=94.29	<0.0001
PAL	$F_{2,643}$=2.87	=0.0575
MAXL	$F_{2,622}$=4.19	=0.0155
CV	$F_{2,654}$=26.20	<0.0001
JF	$F_{2,655}$=3.88	=0.0211
IF	$F_{2,623}$=37.15	<0.0001

To further validate the clustering of the 3 rumble types, a linear mixed effects model was run for each of the acoustic parameters, which were set as the dependent variable. Rumble type was set as an independent fixed effect and recording session was set as an independent random effect. A recording session was a session during which rumbles and group behaviours were recorded continuously with no interruptions. Recording session was used as the random effect in the mixed effects model to control for any likely correlations between rumbles produced around the same time. Of the 19 acoustic parameters, 5 did not meet the assumptions of the parametric test and were therefore not included in the analysis. Of the remaining 14 parameters, 13 had a P value <0.05 (see Table 3) indicating that there were significant differences between rumble types for these parameters. A Tukey's multiple pair-wise comparison was run on those 13 significant parameters to explore which rumble types were different from each other. Table 4 lists the Least Squares Means and the Standard Error of the Means, while Table 5 lists the pair-wise comparisons. Of the remaining 13 parameters a total of 10 showed significant differences for all three pair-wise comparisons. For spectrogram examples of the three rumble types see Figures 5 through 7.

To determine whether specific group behaviours were associated with particular rumble types a multinominal logistic regression was run. The 5 broad group behaviours used were "socializing" (when the recording was of a congregation of family herds, or if the herd was interacting socially while drinking), "resting" (group stationary in

TABLE 4
Least squares means and standard error of the means for each of the three rumble types, for the 14 acoustic parameters subjected to a linear mixed effects model. To convert frequency values to their equivalent in the fundamental frequency simply divide frequency measures by 2.

Parameter	Rumble Type	Mean	Standard Error
FF [a]	1	26.0136	0.3908
	2	38.0452	0.8238
	3	30.9386	0.4462
MIN	1	23.7946	0.4975
	2	34.4319	0.7026
	3	27.1666	0.4792
MAX [a]	1	30.7822	0.3466
	2	48.4842	0.7786
	3	37.1878	0.4027
MEAN [a]	1	27.7139	0.4090
	2	41.6928	0.7103
	3	32.5527	0.4269
PAF [a]	1	26.6880	0.3491
	2	39.5101	1.1280
	3	31.3578	0.4613
FR	1	7.2024	0.2064
	2	15.2433	0.3142
	3	10.4402	0.1963
MAX/MEAN [a]	1	1.1157	0.0042
	2	1.1751	0.0072
	3	1.1490	0.0043
MEAN/MIN [a]	1	1.1729	0.0066
	2	1.2369	0.0116
	3	1.2140	0.0067
DUR [a]	1	4.1319	0.1026
	2	2.2661	0.1149
	3	3.0708	0.0843
PAL	1	0.5004	0.0177
	2	0.5026	0.0278
	3	0.5478	0.0167
MAXL [a]	1	0.4804	0.0178
	2	0.4126	0.0287
	3	0.4212	0.0168
CV [a]	1	2.9881	0.1585
	2	5.1788	0.3173
	3	3.7149	0.1681
JF [a]	1	6.1362	0.1567
	2	5.5068	0.2104
	3	6.1080	0.1488
IF	1	0.6146	0.0058
	2	0.5243	0.0093
	3	0.5836	0.0055

[a] These data were transformed to meet the assumptions of this test. Least squares means and SEM reported here are back transformed.

TABLE 5

Tukey multiple pair –wise comparisons for the 13 parameters that showed significant difference between rumble types.

Parameter	Rumble Types compared	Summary Statistic	Adjusted P value
FF	1 v 2	$T_{660} = -16.73$	<0.0001
	1 v 3	$T_{654} = -11.33$	<0.0001
	2 v 3	$T_{655} = 9.55$	<0.0001
MIN	1 v 2	$T_{660} = -14.72$	<0.0001
	1 v 3	$T_{651} = -6.95$	<0.0001
	2 v 3	$T_{651} = 10.57$	<0.0001
MAX	1 v 2	$T_{660} = -27.24$	<0.0001
	1 v 3	$T_{653} = -16.86$	<0.0001
	2 v 3	$T_{653} = 16.70$	<0.0001
MEAN	1 v 2	$T_{660} = -21.03$	<0.0001
	1 v 3	$T_{651} = -11.58$	<0.0001
	2 v 3	$T_{652} = 13.92$	<0.0001
PAF	1 v 2	$T_{656} = -15.77$	<0.0001
	1 v 3	$T_{657} = -10.73$	<0.0001
	2 v 3	$T_{658} = 8.92$	<0.0001
FR	1 v 2	$T_{646} = -23.33$	<0.0001
	1 v 3	$T_{660} = -13.86$	<0.0001
	2 v 3	$T_{660} = 14.52$	<0.0001
MAX/MEAN	1 v 2	$T_{641} = -7.91$	<0.0001
	1 v 3	$T_{660} = -6.69$	<0.0001
	2 v 3	$T_{660} = 3.51$	=0.0014
MEAN/MIN	1 v 2	$T_{612} = -5.20$	<0.0001
	1 v 3	$T_{657} = -4.99$	<0.0001
	2 v 3	$T_{658} = 1.86$	=0.1506
DUR	1 v 2	$T_{648} = 12.65$	<0.0001
	1 v 3	$T_{660} = 9.93$	<0.0001
	2 v 3	$T_{660} = -6.18$	<0.0001
MAXL	1 v 2	$T_{578} = 2.09$	=0.0937
	1 v 3	$T_{649} = 2.66$	=0.0220
	2 v 3	$T_{653} = -0.27$	=0.9599
CV	1 v 2	$T_{644} = -7.16$	<0.0001
	1 v 3	$T_{660} = -3.84$	=0.0004
	2 v 3	$T_{660} = 4.75$	<0.0001
JF	1 v 2	$T_{649} = 2.62$	=0.0246
	1 v 3	$T_{659} = 0.17$	=0.9842
	2 v 3	$T_{659} = -2.61$	=0.0248
IF	1 v 2	$T_{581} = 8.55$	<0.0001
	1 v 3	$T_{650} = 4.28$	<0.0001
	2 v 3	$T_{654} = -5.79$	<0.0001

clusters and not feeding or socializing), "moving" (group actively moving in a specific direction and not feeding), "agitated" (group visibly disturbed by such things as planes flying overhead, a game capture occurring in the area, etc), and "feeding" (group actively feeding; this was the most common group behaviour). Two regressions were run in

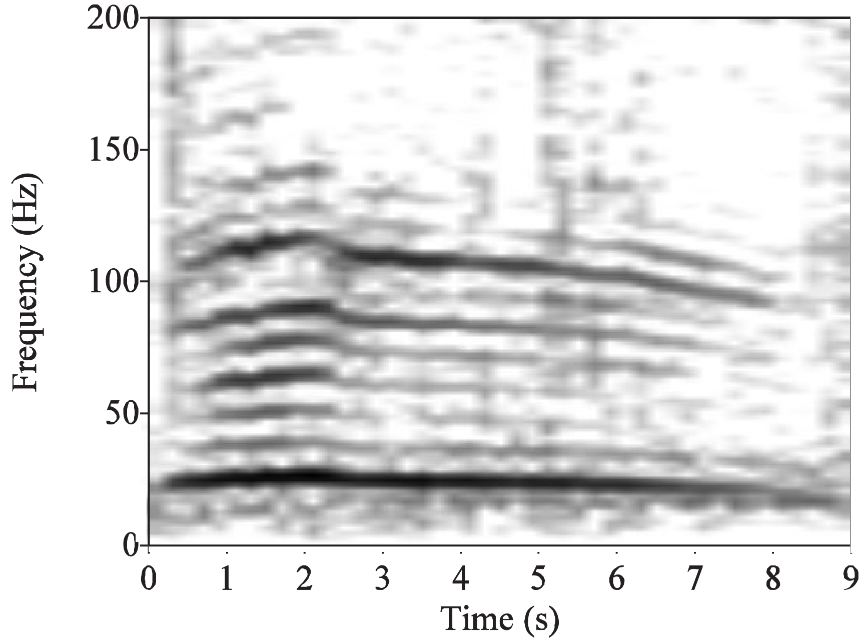

Figure 5. Spectrogram showing an example of a Rumble Type 1. Created in Praat (sampling rate 16,000 Hz, FFT 8192, duration 8.6 s, mean frequency of second harmonic 23 Hz).

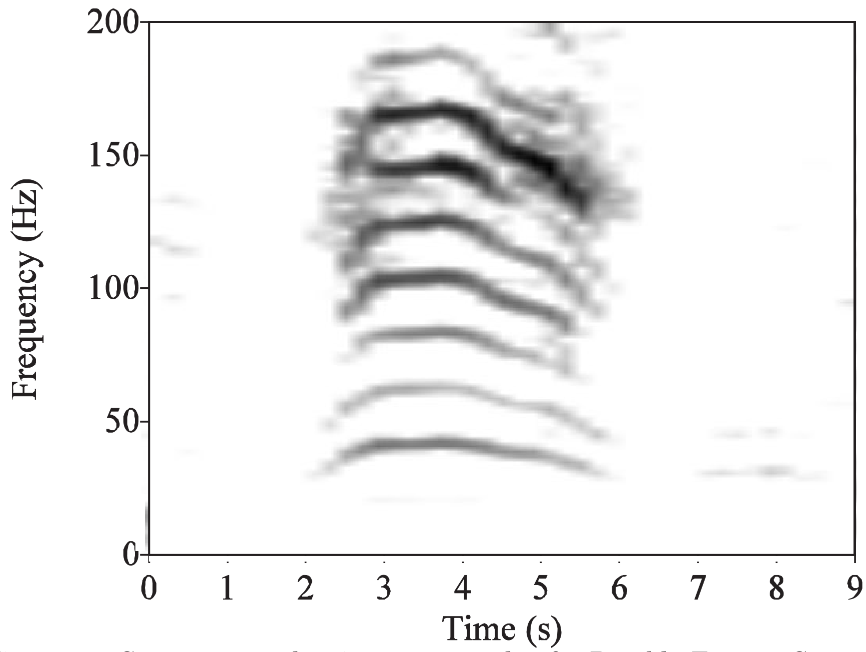

Figure 6. Spectrogram showing an example of a Rumble Type 2. Created in Praat (sampling rate 16,000 Hz, FFT 8192, duration 4.6 s, mean frequency of second harmonic 37 Hz).

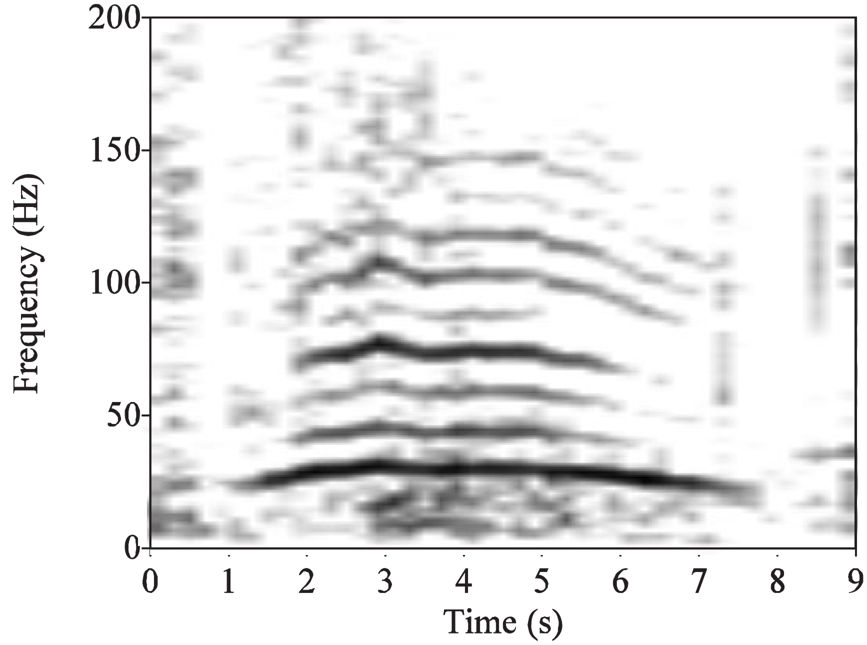

Figure 7. Spectrogram showing an example of a Rumble Type 3. Created in Praat (sampling rate 16,000 Hz, FFT 4096, duration 6.3 s, mean frequency of second harmonic 27 Hz).

order to compare the occurrence of all rumble types for each behaviour. Rumble type 2 and 3 were set as references for the two separate regressions while agitation was used as the behavioural referent for both. There was a significant association of rumble type to group behaviour (χ^2 = 34.11, P<0.0001). The results are listed in Tables 6 and 7. Rumble type 1 and 3 are more closely associated with feeding and resting, while rumble type 2 is associated with agitation and socializing. For an indication of the number of rumbles of each type per group behaviour see Table 8.

The final analysis (a discriminant analysis) was conducted to see how well behaviour could be predicted by using the acoustic parameters. Several acoustic parameters were dropped from the analysis because of their high correlation to other parameters (MIN, MAX, FR). Using the remaining 16 parameters, the discriminant analysis was able to place rumbles in the correct behaviour on average 36% of the time. This is higher than would be expected (20% given that there are 5 behaviours). The proportion correct was even higher when we split the results of the discriminant analysis by rumble type and the behaviour associated by the regression analysis. The proportion correctly attributed by the discriminant analysis to feeding and resting for rumble type 1 was 48 and 50%, while the equivalent figures for agitation and socializing for rumble type 2 was 76 and 50%. The

TABLE 6

Output of multinominal logistic regression with agitation and rumble type 2 set as references.

Rumble Type	Behaviour	Coefficient	Standard Error	Z	P value	lower 95% CI	upper 95% CI
1	feeding	1.684	0.364	4.63	0.000	0.970	2.398
1	moving	0.904	0.566	1.60	0.110	–0.206	2.014
1	resting	1.693	0.593	2.85	0.004	0.530	2.856
1	socializing	0.124	0.530	0.23	0.815	–0.914	1.163
1	constant	–0.211	0.326	–0.65	0.517	–0.851	4.281
3	feeding	1.246	0.333	3.74	0.000	0.594	1.898
3	moving	0.288	0.558	0.52	0.606	–0.805	1.380
3	resting	1.358	0.570	2.38	0.017	0.241	2.475
3	socializing	0.596	0.451	1.32	0.187	–0.289	1.481
3	constant	0.251	0.291	0.86	0.388	–0.319	0.822

TABLE 7

Output of multinominal logistic regression with agitation and rumble type 3 set as references.

Rumble Type	Behaviour	Coefficient	Standard Error	Z	P value	lower 95% CI	upper 95% CI
1	feeding	0.439	0.325	1.35	0.177	–0.198	1.075
1	moving	0.617	0.501	1.23	0.218	–0.364	1.598
1	resting	0.335	0.426	0.79	0.432	–0.500	1.169
1	socializing	–0.472	0.472	–1.00	0.317	–1.396	0.453
1	constant	–0.463	0.310	–1.49	0.135	–1.069	0.144
2	feeding	–1.246	0.333	–3.74	0.000	–1.898	–0.594
2	moving	–0.288	0.558	–0.52	0.606	–1.380	0.805
2	resting	–1.358	0.570	–2.38	0.017	–2.475	–0.241
2	socializing	–0.596	0.451	–1.32	0.187	–1.481	0.289
2	constant	–0.251	0.291	–0.86	0.388	–0.822	0.319

TABLE 8

Number of occurrences of each rumble type during each group behaviour.

	Agitated	Feeding	Moving	Resting	Socializing	Total
1	17	205	14	22	11	269
2	21	47	7	5	12	92
3	27	210	12	25	28	302
Total	65	462	33	52	51	663

discriminant analysis was not as successful at predicting associated group behaviour for rumble type 3 (feeding = 27%, resting = 32%).

DISCUSSION

Using both the shape (contour) of the rumbles as well as 19 acoustic parameters we found the best number of clusters ranged from 2 to 6 rumble types, with 3 being the strongest overall candidate, using the acoustic parameters. Furthermore 10 of the acoustic parameters, a majority of the measures, had significant differences between the 3 rumble types. While some of these acoustic parameters are correlated (e.g. MEAN, MIN, MAX, FR), there is strong evidence that there are differences between rumble types based on several distinct criteria. These criteria include frequency, amplitude, duration and frequency modulation. There were also significant associations between group behaviour and rumble type. Rumble type 1 is a low frequency, long duration rumble with little frequency modulation (mean frequency of 27.7 Hz, duration 4.1 seconds, frequency range 7.2 Hz), which is associated with feeding and resting. Rumble type 2 is a high frequency, short duration rumble with a fair amount of frequency modulation (mean frequency of 41.7 Hz, duration 2.3 seconds, frequency range 15.2 Hz) and is associated with agitation and socializing. Rumble type 3 is of intermediate frequency, duration and modulation (mean frequency of 32.6 Hz, duration 3.1 seconds, frequency range 10.4 Hz) and is associated with feeding and resting. In broad terms this scheme follows motivation-structural rules (Morton 1977) where one would expect higher frequency calls when the animals feel threatened or are more excited. It is also interesting to note (at least in terms of internal validation) that the discriminant analysis was able to assign rumbles to group behaviour more often than by chance alone and that this proportion correct was much higher for the behaviours specifically associated with rumble types (at least for rumble type 1 and 2). The reason this number is lower for rumble type 3 may be because it is an intermediate rumble and therefore harder to discriminate.

Our conclusions tend to agree with those of Leong et al. (2003), differing only in that we found stronger evidence of clustering using acoustic parameters as opposed to the cross-correlation technique used by Leong et al. (2003). We found evidence for a similar number of rumble types although our rumble types tend to be higher in frequency and shorter in duration (to compare our frequency measures with Leong et al.'s frequency measures simply divide our figures by 2 since we used the second harmonic instead of the fundamental). This difference could be attributed to the fact that they may be different vocalizations, or variation between populations of elephants, or it could be variation due to different stimulation levels between captive and wild elephants. Following motivation-structural rules one would predict that the elephants subjected to more stimulation (the wild herds) would have higher frequency calls, on average.

By comparing our rumble types with group behaviours we are able to show that there is some biological validity to this clustering. Although this coding is neither unique nor specific (Bradbury & Vehrencamp 1998) one must remember that this analysis was done without knowing which individual gave which call nor what the individual's specific behaviour was. At the "group" level there is nonetheless strong evidence for clustering and association with behaviours. Because we now have a clearer picture of how elephants might be distinguishing different calls, researchers will be in a better position to test how individual elephants differentiate between call types. By playing back calls that have known contexts and effects on other elephants and by artificially varying these calls using the parameters that led to strong clustering (e.g. one of the measures of frequency, duration, amplitude and frequency modulation), one should be able to determine which parameters are used by the elephants to distinguish between call types. It should also be noted that there are other measures of acoustic properties that could also be used by elephants in distinguishing between call types. These might include such parameters as the number of higher harmonics or the relative amplitude of different sets of harmonics (i.e. formants, which are energy bands in the spectrum corresponding to vocal tract resonances). We did not analyze these in this paper as we were not able to identify which individual elephant produced each rumble. As such we had no way of knowing if the number of higher harmonics or formants was caused by source filters or by environmental effects on the sound propagation (e.g. differential attenuation of different frequencies). McComb et al. 2003 successfully used source filter measurements (the frequency of the first and second formants) in discriminating between the individual identity of calling elephants although they also used source related variables like the ones used in this paper (mean, max, min frequency, duration). Nonetheless, source filter variables may play an important part in discriminating between call types; as such they should also be incorporated into playback experiments.

This paper has focused on the acoustic variation within a group of African elephants. Acoustic variation has been shown to occur at many different levels. Geographic variation between isolated populations has been detected in bearded seals (Cleator et al. 1989), Weddell seals (Thomas & Stirling 1983), and sperm whales (Weilgart & Whitehead 1997). Regional dialects occur in the yellow-naped amazon (a parrot) (Wright 1996), while group or matrilineal/kin dialects occur in greater spear-nosed bats (Boughman & Wilkinson 1998), killer whales (Ford & Fisher 1983), and pigtail macaques (Gouzoules & Gouzoules 1990). Individual variation has also been shown in rhesus macaques (Rendall et al. 1996, Hauser 1991), Belding's ground squirrels (McCowan & Hooper 2002), and spectacled parrotlets (Wanker et al. 1998). This study shows that there is enough physical variation within the calls of this group of elephants to distinguish different rumble types. It remains to be seen which form of variation is used by African elephants to distinguish between call types.

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