Repetitive interactive vocal bouts facilitate group coordination in African elephants (*Loxodonta Africana*)

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ABSTRACT

Interactive vocal bouts coordinate movement within African elephant family groups. Groups call interactively ($p < 0.0001$) within a series of overlapping vocal bouts that increase significantly upon initiation of movement ($p= 0.014$), bouts increasing as a function of herd size ($p = 0.03$), thus larger herds may need more coordination. Interactive bouts may also facilitate group cohesion, bonding, inter-group spacing and signal detection, as overlapping calls effectively lengthen signals by three times ($p = 0.834$). The repetition of these longer signals would increase the signal to noise ratio (SNR) and reduce the noise floor for elephants listening at a distance.

I. INTRODUCTION

Coordinated vocalizations such as duetting and chorusing have evolved in the communication patterns of many species. The evolution of duetting behavior is most common in species which form long term associations and/or benefit from such cooperative displays (Serpell 1981). These vocalizations assist in strengthening or forming pair bonds in gibbons (Geissmann 1986; Mitani 1985a; Cowlishaw 1992) and monogamous birds (Farabaugh 1982). They function as territorial advertisements and maintain intergroup spacing in gibbons, toads, birds, and wolves (Hultsch 1983; Mitani 1985a & b; Hoglund and Robertson, 1988; Harrington 1989). In birds, females sing to maintain family group bonds and to defend territories (Ritchison 1983; Seutin 1987; Yasukawa 1989; Cooney and Cockburn 1995). Anti-predator warning (Tilson and Norton 1981; Hauser 1987), mate attraction (Levin 1996), group bonding (Brown and Farabaugh 1991) and group movement (Radford, 2004) are among their other functions, as well as the possibility of forcing a mate to be attentive (Smith 1994). Chimpanzees use duetting to establish allies and recognize individuals (Mitani and Brandt 1994).

Elephants maintain strong family bonds facilitated by short and long distance communication (Payne and Langbauer 1992). In the short range, tactile, chemical, visual and acoustic cues are used to strengthen family bonds and assess individual health (Payne and Langbauer 1992). Long range communication through infrasound (Poole et al. 1988; Poole 1999; McComb et al. 2000) and, potentially, seismic cues (O'Connell-Rodwell et al. 2000; Gunther et al 2004; O'Connell-Rodwell et al. 2006) may allow for the coordination of movements of widely separated groups of elephants. Female elephants are thought to engage in coordinated vocalizations to maintain contact, spatial coordination, and for mate finding and in the context of reproduction (Poole et al. 1988). 'Contact' calls reveal group identity within a 1 km range (McComb et al. 2003), thus coordinated vocalizations may serve different purposes within short and long range contexts.

Although much has been written about chorusing and duetting, few have addressed patterns that are more interactive or 'conversational' in nature. Studies of interactive communication in a group of three pygmy marmosets showed that there were orderly turn-taking patterns in their sequences of calls (Snowdon and Cleveland 1984), allowing individuals to monitor the location and presence of other group members (Snowdon and de la Torre 2002).

This study was designed to determine whether elephant family groups are more likely to vocalize in an interactive turn-taking manner and what role these interactive vocal bouts play in coordinating group action. Interactive vocal bouts are distinguished from calls others have defined as chorusing or duetting in that, usually more than two individuals are involved and calls are not given at the same time (not synchronous), but rather fall within predictable patterns with calls following each other with very little to no overlap between calls, as compared with chorusing which implies temporal synchrony, and duetting which implies the participation of only two individuals. These bouts are also not associated exclusively with either reproduction or territorial aggression, but seem to be involved in group coordination.

II. METHODS

A. Data Acquisition

At each of five waterhole locations in Etosha National Park, Namibia, audio recordings and field observations were made over the period of July-August, 1994 and July 1995. Whenever feasible, recordings were continuous throughout an elephant herd's presence at a waterhole. Audio recordings were made using a TEAC digital recorder with a frequency response of 20-20,000 Hz and a Neumann KM131 omni-directional microphone with a flat frequency response of 20-20,000 Hz. All recordings were made at a distance of 5m to 15m from the waterholes. Time of day, herd size and composition, individual and group behaviors, and specific identifiable rumble types (i.e., Let's Go) were noted with the audio recordings.

B. Data Preparation

A total of 28 waterhole visits, containing 1028 rumbles, were collected within 14.8 hours of field recordings from 14 different family groups (based on herd composition and number of individuals). Using the sound program Cool Edit Pro, all audio recordings were converted into wav files and viewed as continuous spectrograms. We defined time periods as *episodes*, beginning with 1) the arrival of a family group at the waterhole or 2) the beginning of a recording session where a herd is already present at the waterhole. An episode ends either 1) fifteen minutes after the herd first initiates leaving a waterhole (with initiation defined as the first Let's Go vocalization or physical movement away from the waterhole) or 2) after the herd has completely left the waterhole to a distance of at least 100 m (whichever comes first). The fifteen minute limitation was used in cases when herds were slow to depart or when field notes failed to record exactly when herds departed. Departure was initiated when a matriarch emitted a 'Let's Go' vocalization (Poole et al., 1988) or stood still in readiness to leave from the water hole, or at least one individual began to leave the area.

The duration of episodes, duration of single rumbles and bouts, the number of herds and herd sizes and the time of the beginning of departure were calculated. Episodes containing intra and conspecific aggression or disturbances, which tended to increase the rate of calling, were not included in this analysis. Acoustic characteristics of rumbles were examined using the SpectraPLUS 2.32 sound program.

C. Data Analysis

The temporal spacing and physical characteristics of the vocal repertoires produced prior to and during elephant herd departures from waterholes were analyzed in MINITAB (v 13), unless otherwise noted. Information regarding episode duration, rumbles per episode, herd size, and departure period duration were summarized with descriptive statistics.

D. Temporal Organization

From all 28 episodes analyzed, 14 episodes of 14 separate family groups containing 254 vocalizations were selected for individual analysis of rumble temporal organization based on our requirement that these episodes lacked disturbances, confounding factors of more than one herd present, and contained specific notes on the herd number, arrival and departure times. Based on a log survivorship analysis, rumbles were separated into two different temporal categories, rumbles made within an interactive bout, and 'non-interactive' rumbles.

Log survivorship analysis determines the minimum interval separating successive vocalizations by plotting the time interval between successive occurrences of vocalizations against the logarithm of the number of intervals greater than that time interval (Slater and Lester 1982). The Bout Criterion Interval (the cutoff point differentiating within from between bout intervals) was determined by finding the steep change in slope (Figure 1). According to this criteria, every rumble that was less than 1.5 s from another rumble was considered to have been delivered in an interactive bout, and every other rumble was considered a 'non-interactive' rumble. Thus interactive bouts are operationally defined in our study as a group of consecutive, overlapping or contiguous calls emitted less than 1.5 s apart.

The temporal patterning of vocalizations during the waterhole visits was measured using a Kolmogorov-Smirnov test in Matlab (v.7.0.1) to determine if vocalizations were randomly distributed in time throughout the duration of the visit. A cumulative distribution function was generated using the inter-rumble interval period (N=240) and compared to a theoretical distribution where the data were randomly distributed (in this case an exponential distribution).

Each waterhole visit was divided into two periods, pre initiation of departure, and post initiation of departure. A Wilcoxon Signed Rank test was run comparing the rumble rate during the pre and post periods. In order to demonstrate that the number of rumbles per bout, the number of bouts, and the duration of the post period all have an effect on rumble rate in the post period, a multiple regression was run with rumble rate as the dependent variable and number of rumbles per bout, number of bouts, and duration of post period as the independent variables. Given that these three variables directly affect rumble rate, each variable was tested individually to determine which changed between the pre and post periods. Since not all herds had a bout of rumbles in both the pre and post periods, only trials that contained bouts in both periods were included when testing for differences in the number of rumbles per bout. Because more bouts would be expected in a longer period, the number of bouts in the pre and post periods were normalized by dividing by the duration in seconds of that period. The relationship between herd size and the number of interactive bouts in the pre and post departure period was also tested.

III. RESULTS

The general characteristics of the selected 14 episodes are summarized in Table 1.

A. Temporal Organization

Vocalizations emitted by herds during waterhole visits are not randomly distributed in time (Kolmogorov-Smirnov: $D = 0.446$, $p < 0.0001$; n=240 inter-call intervals within 14 episodes). Indeed, almost 2/3rds of the rumbles were made within interactive bouts (165 interactive rumbles vs 89 non-interactive rumbles). The rate of calling significantly increased after the initiation of departure when compared to the period before the initiation of departure (Wilcoxon Signed Rank test: Wilcoxon T Stat = 15.0*, $p = 0.02$*; n=14 episodes involving 254 calls). The proportion of interactive rumbles increased from 55.6% to 70.2% in the post initiation of departure period. Because we found a significant difference, we ran a comparison of rumble rate between pre and post initiation of departure periods using only interactive and then non-interactive rumbles. Since this analysis involved two separate tests, a Bonferonni correction was applied and only a p value of less than .025 was accepted as significant. Only interactive rumble rates increased significantly (N=14, Wilcoxon T Stat = 14, $p = 0.017$), while non-bout rumbles did not (N=14, Wilcoxon T Stat = 26.0, $p = 0.103$).

The number of rumbles per bout, the number of bouts and the duration of the post initiation of departure period all had an effect on the rumble rate in the post period (Multiple Regression: $F_{3,10} = 89.35$, $p < 0.001$), all variables explaining 95% of the variance in rumble rate (adjusted $R^2 = 95.3\%$). The number of rumbles within an interactive bout did not vary between prior and post departure periods (N=7, Wilcoxon T stat = 12.0, $p = 0.834$), remaining constant at an average of three. The number of bouts in the pre and post periods were then normalized, showing that the number of bouts increased significantly in the post period (N=14, Wilcoxon T stat = 13.0, $p = 0.014$). The duration of the pre and post initiation of departure periods did not differ significantly (N=14, Wilcoxon T stat = 67.0, $p = 0.379$). In addition, the number of bouts in the post period increased with herd size ($F_{1,12} = 6.10$, R^2 adjusted = 28.2%, $p = 0.030$; Figure 3a), while there was no correlation between herd size and the number of bouts in the pre departure period ($F_{1,12} = 0.34$, R^2 adjusted = 0.0%, P = 0.568; Figure 3b). Herd size ranged from 6 to 31 with an average size of 14.9.

54 interactive bouts within the 14 selected episodes were examined. The bouts per episode, number of calls per bout, and various rumble rates are summarized in Table 2. The average duration of all interactive bouts was 8.51 (*SD* 4.28) sec and the average number of calls per bout was 3.17 (*SD* 1.42) calls. Since these calls are given with little or no time gaps, the signals increase an average by a factor of 3.17 which has the effect of decreasing the noise floor and therefore increasing the signal to noise ratio (SNR). This same phenomenon is seen when analyzing sounds with Fourier transforms. When one increases the length of the analysis window (the FFT size), one not only increases the frequency resolution but also decreases the noise floor and improves SNR. In this particular case the improvement in amplitude above the noise floor should be around 1.78 ($\sqrt{3.17}$) which translates into an increase of 5 dB in the SNR ($20*\log_{10}(1.78)$). The average number of bouts per episode was 3.86 (SD 2.38) with 33.3% of the total bouts occurring prior to the initiation of departure and 66.7% occurring post initiation.

IV. DISCUSSION

Elephant family groups vocalize more often in bouts, where calls are more likely to occur in a series of calls (with little to no overlap) than be given alone. These 'interactive' bouts increase in number after the initiation of departure and thus appear to facilitate group coordination. Since there is a significant positive relationship between the number of interactive bouts and the size of the family group upon initiation of departure, larger groups may need more coordination to leave an area. Since the number of rumbles per bout is very stable at around 3 rumbles, regardless of group size, group coordination may be maintained by only a few individuals.

These bouts create a signal that is 3 times longer than a signal produced by one individual which serves to increase the signal to noise ratio (SNR) and reduce the noise floor, making it easier to detect and process a signal at greater distances. Furthermore, during departure, the bouts are repeated at a greater rate. With multiple bouts, listening elephants at a distance would have an opportunity to optimize their physical position to better resolve the signal; they could conceivably accumulate more detail on subsequent presentations of the signal.

The repetition of calls in Weddell seals is also thought to enhance signal detection over long distances and during times of high background noise (Moors and Terhune 2004), which is also thought to be the case for whales (Payne 1995). Foote et al. (2004) found that killer whales increased the duration of their calls due to increases in background noise caused by increased boat vessel traffic. This finding is supported by physiological studies showing that auditory thresholds appear to be based on temporal summation, thus longer signals should reduce the noise floor, facilitating signal detection (Heil and Neubauer 2003). In human hearing experiments, repeated signals appeared to facilitate detection as well (Garner 1947; Hamilton 1957; Greenwood 1961).

Freezing behavior has been described in elephants in the context of scanning with the ears for acoustic signals (Langbauer et al. 1991). We have noted that elephants freeze for long periods within and between interactive vocal bouts (unpublished result) suggesting that they might be "listening to" these long repeated signals in an inherently noisy environment, either with their ears or seismically through their feet. In addition, it appears that temporal patterning of calls is an important signal, where the number of interactive bouts increases with initiation of departure from the water hole and with herd size. Thus eavesdroppers might learn of the availability of a resource at greater distances which would facilitate inter-group spacing.

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Figure Legends:

Figure 1. Log survivorship analysis plot. By plotting the inter rumble interval against the log of the number of intervals greater than that time interval, one is able to determine the bout criterion interval by the sudden change in slope (in this case at ~ 1.5 s).

Figure 2. A series of rumbles given by a herd after the initiation of departure over a period of 240 sec (from left to right). Example of interactive bouts versus non-interactive calls are highlighted. The last trace shows the interactive bouts continuing between herd members in the distance (distinguished by the attenuation of the higher harmonics.)

Figure 3a. The number of bouts per second after initiation of departure versus the number of individuals within the herd. The regression lines show a significant positive relationship between the two variables and explain 28% of the variance in the data.

Figure 3b. The number of bouts per second prior to the initiation of departure versus the number of individuals within the herd. The regression lines show no correlation between number of bouts and number of individuals.

Table 1: Summary of episodes used in the analyses (N = 14).

Episode Duration (h:mm:ss)	Mean (SD)	0:21:11 (0:08:04)
	Median	0:17:55
	Range	0:10:49– 0:40:36
	Total	4:56:34
Rumbles per Episode	Mean (SD)	18.14 (9.45)
	Median	17
	Range	5 - 36
	Total	254

Table 2. Summary of rumble data including bout and non-bout rumbles.

		Before initiation of departure	After initiation of departure
Rumble rate	Mean (SD)	0.506 (0.484)	1.324 (1.052)
	Median	0.33	1.00
Interactive rumble rate	Mean (SD)	0.2935 (0.3602)	0.948 (0.866)
	Median	0.13	0.64
Non-interactive rumble rate	Mean (SD)	0.2120 (0.1744)	0.3761 (0.2572)
	Median	0.20	0.40
Rumbles per bout	Mean (SD)	3.17 (1.42)	3.08 (1.08)
	Median	3	3
Total # bouts		18	36
Bouts per second	Mean (SD)	0.0015 (0.0017)	0.0051 (0.0046)
	Median	0.001	0.0036
Duration (s)	Mean (SD)	728 (517)	552.9 (289.4)
	Median	632	555

Figure 1.

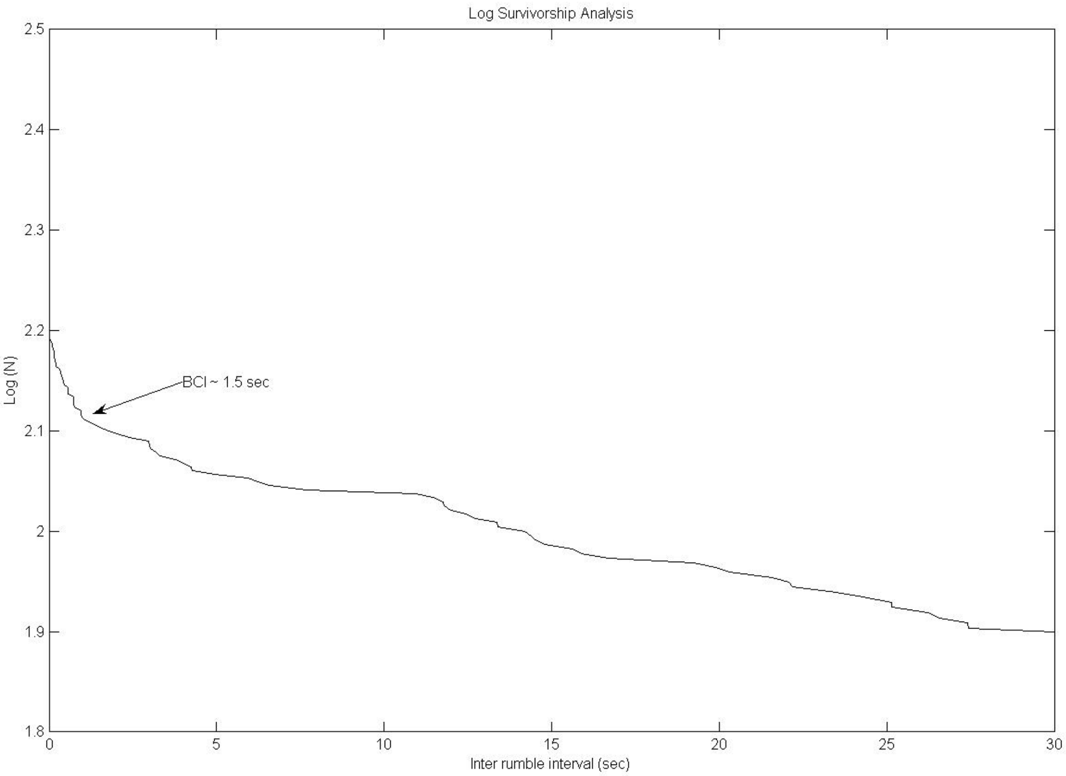
Log Survivorship Analysis
Log (N)
2.5
2.4
2.3
2.2
2.1
2
1.9
1.8
BCI ~ 1.5 sec
0
5
10
15
20
25
30
Inter rumble interval (sec)

Figure 2.

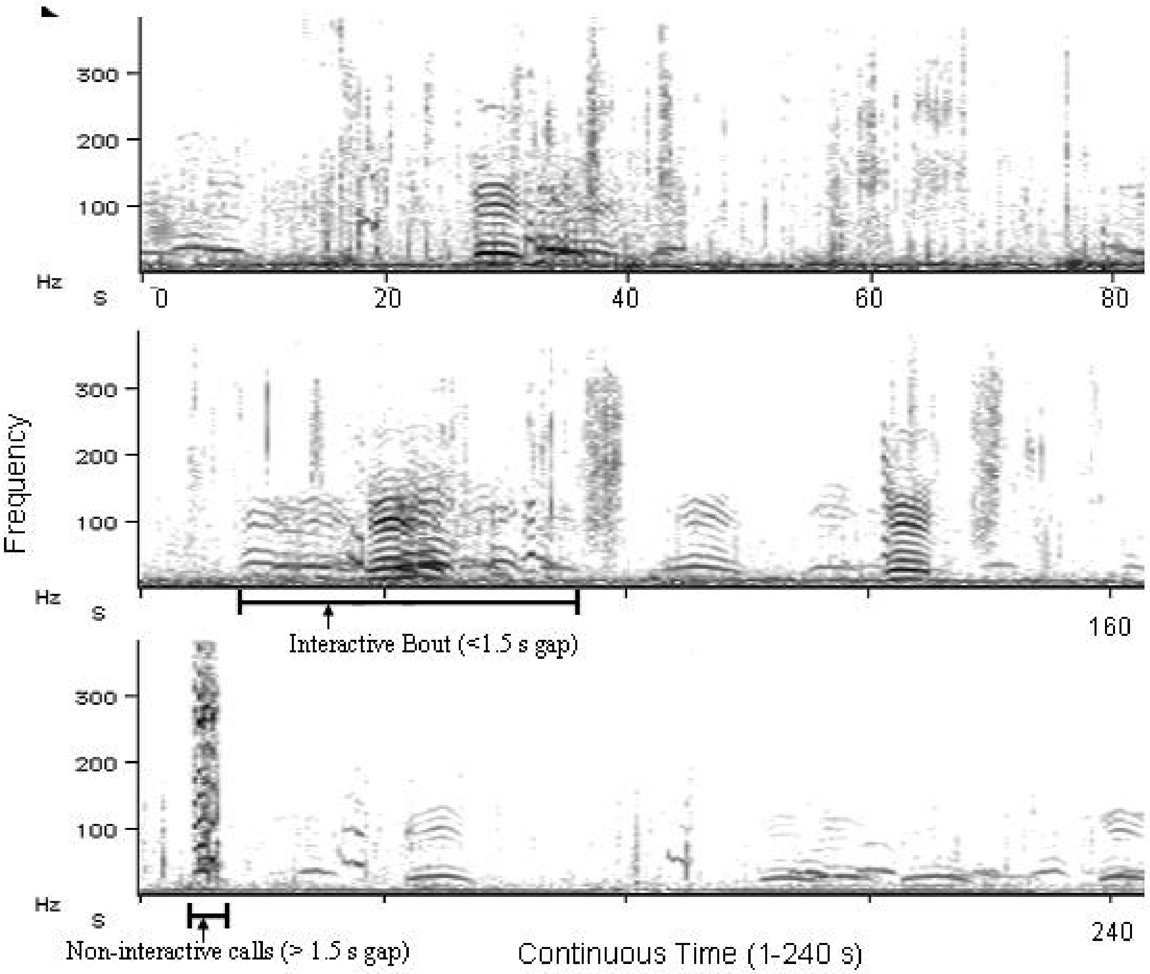
Frequency
Hz
s
300
200
100
0
20
40
60
80
160
240
Interactive Bout (<1.5 s gap)
Non-interactive calls (> 1.5 s gap)
Continuous Time (1-240 s)

Figure 3a.

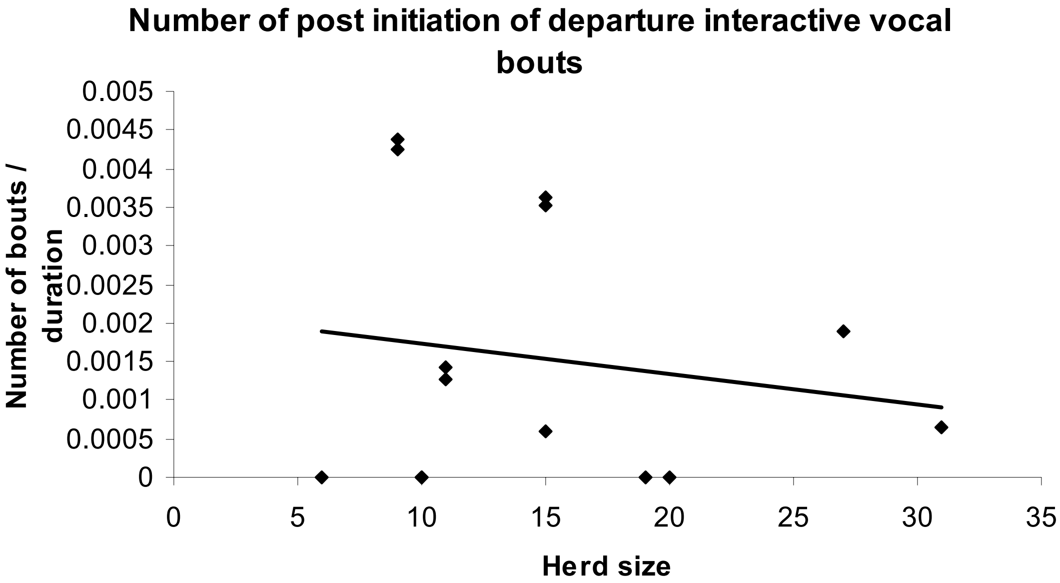

Figure 3b.