

## AFRICAN ELEPHANTS RESPOND TO DISTANT PLAYBACKS OF LOW-FREQUENCY CONSPECIFIC CALLS

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### Summary

We conducted 58 playback experiments with free-ranging African elephants in Etosha National Park, Namibia, to estimate the distance over which some of their low-frequency calls are audible to other elephants. We broadcast pre-recorded elephant calls to elephants that were 1.2 and 2.0 km from the speaker while making simultaneous video and audio recordings of their behavior. In order to reduce the risk of habituation, we used a variety of call types as stimuli. Elephants responded to playbacks at both 1.2 and 2.0 km, with a full response consisting of the elephant vocalizing, lifting and spreading its ears, remaining motionless in this position ('freezing'), moving the head from side to side ('scanning') and, in the case of males responding to female estrous calls, orienting to and finally walking 1 km or more towards the loudspeaker.

We analyzed our data quantitatively for three of these responses. The occurrence of each behavior increased substantially immediately after playbacks.

Owing to limitations of the loudspeaker, we were only able to broadcast calls at half the sound pressure level (i.e. -6 dB) of the strongest calls we have recorded. Since sound at the frequencies of these calls is predicted to suffer from little, if any, attenuation in excess of that caused by spherical spreading, we estimate these calls to be audible to elephants at least 4 km from the source (twice the distance over which we documented responses).

These results are consistent with the hypothesis that the very low-frequency calls of elephants function in communication between individuals and groups of elephants separated by distances of several kilometers.

### Introduction

The purpose of this study was to estimate the distance over which African elephants (*Loxodonta africana*) can perceive the low-frequency calls of conspecifics, as part of an effort to determine whether these calls are used in long-distance communication (Payne *et al.* 1986; Poole *et al.* 1988).

These calls, which have fundamental frequencies of 15–35 Hz and sound pressure levels as high as 117 dB SPL 1 m from the source (Payne *et al.* 1986; Poole

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*et al.* 1988), constitute a large proportion of the vocal repertoire of both African and Asian elephants (*Elephas maximus*). [All sound pressure measurements in this paper were taken in the far field (more than 10m from source) and extrapolated, assuming spherical spreading, to the standard 1m reference distance.] Elephants have excellent hearing in this portion of the acoustic spectrum (Heffner and Heffner, 1980: these measurements were made on an Asian elephant but are likely to hold true for African elephants as well). At distances of more than a few meters, many of the low-frequency calls are entirely inaudible to the human ear, but some have higher-frequency components that people hear as low, soft rumbles. The calls appear well suited for transmission over long distances since low-frequency sound propagates more effectively than sound at higher frequencies (Ingard, 1953; Beranek, 1971; Waser and Waser, 1977; Marten and Marler, 1977; W. R. Langbauer, R. A. Charif and F. Osborn, unpublished data).

Long-distance acoustic communication would help explain some enigmatic aspects of elephant social behavior. For example, Martin (1978, personal communication) has found that radio-collared elephants in separate cow-calf groups often exhibit coordinated movement over periods of many hours or even days, despite being separated by distances of several kilometers. In some cases, this coordination takes the form of maintaining parallel movement tracks, with changes in direction being synchronous between groups. In other cases, widely separated groups simultaneously and abruptly change direction and move directly towards each other, eventually meeting.

Long-distance communication is also apparently involved in the ability of mature males to find mature females during the females' extremely brief periods of estrus. Adult male elephants spend most of their time apart from females. They compete for access to estrous females (Poole, 1982; Hall-Martin, 1987), which are scarce, owing to the short duration (2-4 days) of estrus and the typically long interval (4 years) between estrous periods caused by pregnancy and lactation (Moss, 1983). Furthermore, the occurrence of estrous females is unpredictable in time and space, because of their asynchronous estrous periods and large home ranges. Yet estrous females are rapidly located by males, which gather from many directions.

We propose that low-frequency acoustic signals may be involved in both the ability of separated cow-calf groups to coordinate their movements over long periods, and the ability of mature males to find females during their brief and asynchronous periods of estrus.

As a first step towards testing this hypothesis, we performed a series of playback experiments designed to provide estimates of the distances over which elephants can hear low-frequency conspecific vocalizations.

## Materials and methods

### *Synopsis*

We conducted playback experiments in Etosha National Park, Namibia, in an

area that was closed to park visitors. The study took place in August–October 1987, which is the latter portion of the 7-month dry season. From a 6.5-m tower overlooking a waterhole, we collected simultaneous visual and acoustic recordings of the behavior of elephants when they came to drink. The elephants were individually identified by means of distinctive tusks and by notches on the ears.

We broadcast playback calls from four locations, at two distances and in two directions from the center of the waterhole: 1.2 km to the north, 1.2 km to the south, 2.0 km to the north and 2.0 km to the south. None of these sites was visible from the waterhole, because of intervening trees. The terrain was level throughout the study site.

We conducted 58 playback trials, approximately half of which were directed at males and half at cow–calf groups. In each trial we documented at least 5 min of baseline behavior before playing a brief call sequence from a known distance, and at least 5 min of behavior following the call. We then compared the occurrence of three response behaviors in the periods preceding and following the start of each playback by examining the video and audio tape records of the experiment.

Our experiments were not designed to provide any information about the social significance of particular calls. Although a variety of calls were used as stimuli, sample size limitations prevent us from distinguishing the functions of particular call types. For purposes of simply determining whether calls of a given sound pressure level were audible at a given distance, we regarded different call types as equivalent stimuli.

### *Subjects*

For each experiment, the subjects consisted of all elephants present at the waterhole when the playback was broadcast. Each experiment was classified as being either a ‘male’ trial or a ‘cow–calf group’ trial. In male trials, the subjects were exclusively adult or subadult male elephants, who visited the waterhole singly or in groups of up to eight individuals (mean=3). In cow–calf group trials, the subjects were one or more cow–calf groups, each containing presumably related females and their offspring, occasionally accompanied by one or more subadult or adult male elephants. Sizes of cow–calf groups ranged from three to 24 individuals (mean=15).

The number of elephants visible to us at the tower during a given trial varied from one to over 40. We played calls to 20 individually identified males, five known cow–calf groups (i.e. most of the adults in each group were individually identified and repeatedly found together – corresponding to the ‘family unit’ of Poole and Moss, 1989) and several males and cow–calf groups that we were not able to identify.

To minimize habituation, most stimuli were played only once to a known animal or group at each distance. However, we could only observe animals within a radius of about 1 km of the tower. It is possible that other elephants were sometimes within range of the playback but unobserved by us. If some of our test subjects had been habituated to the playback stimuli because of such unintentional prior

exposure, our results will reflect an underestimate of the responses to the playback.

### *Stimuli*

We selected vocalizations of African elephants that seemed likely to elicit responses from conspecifics over large distances. Previous observations by the authors and studies by others (e.g. Poole *et al.* 1988; J. H. Poole, unpublished data) provided the basis for our selection of stimulus calls.

The calls used as stimuli vary in geographical origin and with respect to the social context in which the calls were made. We chose to use a variety of calls (rather than the same call in all experiments) in order to minimize the risk of habituation to particular calls, as discussed above.

Partially overlapping sets of stimuli were used for males and for cow-calf groups.

#### *Stimulus 1*

An estrous call sequence (see Poole *et al.* 1988) from a female elephant immediately following an unsuccessful mating with a young bull. Recorded by K. Payne and J. Poole in Amboseli Park, Kenya, in 1985. Used in 14 trials for males and one trial for cow-calf groups.

#### *Stimulus 2*

Calls of adult females and possibly a male in musth as he tested the genital areas of one female after another with his trunk. Recorded by the authors in Etosha in 1987. Used in 13 trials for males and six trials for cow-calf groups.

#### *Stimulus 3*

Three calls given by a dominant adult female elephant in a captive group as a keeper arrived with food. Responses to the original call included vocalization, orientation, moving towards the caller and clustering of the artificial family group. Recorded by the authors in the MetroToronto Zoo in 1987. Used in two trials for males and seven trials for cow-calf groups.

#### *Stimulus 4*

Overlapping low-frequency rumbles given by members of an elephant cow-calf group after a calf had given a distress call upon falling into a waterhole. Recorded by the authors in Etosha in 1987. Used in five trials for cow-calf groups.

#### *Stimulus 5*

An interchange of calls recorded at night during the meeting of several cow-calf groups. Recorded by the authors in Etosha in 1987. Used in 10 trials for cow-calf groups.

Each stimulus lasted between 20 and 40s and was broadcast only once in each

playback trial. The peak sound pressure level of the broadcast calls was about 110 dB SPL (extrapolated to 1 m from the source), which is slightly less than half the amplitude (117 dB SPL) of the loudest elephant calls that we have recorded in the field. The loudspeaker that we used was unable to reproduce elephant calls at 117 dB without distortion.

#### *Playback equipment*

Playback stimuli were reproduced using a Nagra IV-SJ tape recorder, an Alphasonik MA-2150 amplifier, a laboratory-built audio equalizer and a specially constructed, two-port loudspeaker which measured 61 cm × 91 cm × 122 cm and contained two JBL 2245H transducers. The frequency response of the speaker was approximately  $\pm 4$  dB over the range 18–150 Hz, the range in which nearly all the energy of the stimulus calls is located (W. R. Langbauer, R. A. Charif and F. Osborn, unpublished data). The speaker was mounted on top of a Volkswagen van, with the midline of the speaker 2.5 m above the ground – the approximate height of an adult elephant's mouth and ears.

#### *Recording equipment*

From the tower, we recorded visible behavior with two video cameras, each connected to a separate Quasar model 5747 video recorder. During daylight hours we used a Panasonic PK-980 camera to follow an individual focal animal, and a low-light RCA model TC-1034 camera to obtain a wide-angle view of the elephant group. During 10-day periods surrounding full moon we were able to use the low-light camera to follow focal groups of animals at night.

To document any vocal responses, we used four wireless microphones distributed in a square array roughly 0.25 km × 0.25 km around the waterhole. Signals from the microphones were transmitted to the tower and recorded on both a TEAC R-61 four-track FM recorder and, after multiplexing, on one audio track of the stereo video recorder. It was thus possible, during analysis, to synchronize our audio and video records. The array of wireless microphones allowed us to monitor a larger area than would be possible by using just one microphone. The frequency response of the multiplexed audio recording system was approximately 10–600 Hz. Since most of the energy in elephant's low-frequency calls is below 150 Hz, this system was adequate for our needs.

#### *Playback procedure*

For each trial, we selected the direction of the playback (north or south) using a random numbers table, but, to be sure of getting some complete data sets even in the event of early rains (and subsequent dispersal of our study animals), we conducted most of the 1.2 km trials before starting the 2.0 km trials.

Playbacks were not attempted during the first 10 min following the elephants' arrival at a waterhole, to give them time to establish their positions at the water's edge and satisfy their initial thirst. Playbacks were also avoided when observers on the tower were aware of any other obvious event to which the elephants might be

attending, such as a calf falling into the water or the arrival of other elephants. One trial, which subsequently appeared to have occurred simultaneously with other events of social significance to the elephants, was omitted from the analysis.

After the above conditions had been met, observers at the tower contacted the personnel at the speaker by walkie-talkie. When wind speeds were less than about  $50 \text{ m s}^{-1}$  (5 knots), the call was broadcast at some point within the subsequent 10 min, with the precise instant of broadcast unknown to the observers at the tower. Under more windy conditions we had to modify this procedure, because of excessive wind noise at the recording microphones. In these trials (about 60 % of the total) the calls were played within 2 min of a signal from the tower, during lulls in the wind around the water hole.

### *Analysis*

At the completion of the field season, we examined our audio and video tapes and compared the behavior of the subject elephants during equal periods immediately before and after each playback. We selected three types of behavior (see below) that appeared to be reliable indicators of response to the playback and could be reliably quantified in our sample. In previous field (Poole *et al.* 1988) and zoo (Langbauer *et al.* 1990) studies we observed that elephants gave these responses to a variety of different calls. Thus, it is likely that these responses can be used as general indicators of perception.

All playbacks to a given type of group (cow-calf groups or male groups) from a particular distance were pooled for analysis, irrespective of which stimulus was played. Although pooling data from playbacks of different calls may obscure differences in the types of response evoked by different calls, it should not lead us to overestimate the distance at which elephants can hear conspecific calls.

For each behavior, some trials could not be scored owing to inadequacies of the video or audio record either before or after the playback; thus, the number of trials scored was not the same for all three response behaviors.

In analyzing visually observable behaviors we only scored animals three-quarters of adult size or larger. We analyzed acoustic responses using spectrograms made on a Spectral Dynamics 301 C-C spectrograph. For each trial, we measured the incidence of each response behavior in the entire group during equal periods immediately preceding and following the start of the playback. When the post-playback period received a higher score than the pre-playback period, the trial was scored as '+' for that behavior; when the post-playback score was lower than the pre-playback score, the trial was scored as '-'; when the pre- and post-playback scores were the same, the trial was scored as 's'.

The three response behaviors and their respective scoring intervals and criteria were as follows.

### *Vocalizing*

Vocalizations that were clearly audible on the videotape sound track or clearly visible on the spectrograms were scored as discrete events. We made no distinction

between different types of calls. Scoring interval: from 1 min preceding to 1 min following each playback. In 15 out of the 58 trials our recordings were adequate to score for vocalizing.

### *Freezing*

During freezing, an individual stood completely still for at least 2 s with no movement of feet or trunk, and with the ears stiffened and spread as if listening. If one or two animals were present, this behavior was scored as a behavioral state of measured duration, and the total duration of pre- and post-playback periods was compared. (Pre- and post-playback intervals in which the durations of freezing were within 2 s of each other were scored as being the same.) For three or more animals, the number of animals freezing before and after the playback was compared. Scoring interval: from 30 s preceding to 30 s following each playback. In 35 out of the 58 trials the recordings were adequate to score for freezing.

### *Moving towards the loudspeaker*

The location of each animal 3 min before the playback was compared to its location at the time of the playback, and the component of its straight-line movement along an axis towards or away from the loudspeaker was estimated in body lengths. Movement of the whole group was assessed by summing the movements of all individuals. Similar measurements were made comparing each animal's position at the start of playback to its position 3 min later. The net motion towards the loudspeaker before and after the playback was compared. (Note that this is a measure of relative movement before and after the playback: a trial could be scored as + even if the animals moved away from the speaker after the playback, as long as the net movement away during the post-playback interval was less than the movement away during the pre-playback interval. This occurred in only one of 42 trials, however.) Scoring interval: 3 min before and 3 min after the playback. In 42 out of the 58 trials the data were adequate to score for movement.

The different intervals used in scoring the different behaviors reflect different latency times for each type of reaction as observed in the field and in our preliminary zoo experiments (Langbauer *et al.* 1990).

In Table 1, each + or – score reflects the net behavior of the group of elephants being observed. This scoring scheme does not distinguish between a direct response to the playback stimulus and a socially facilitated response in which an elephant responds to other elephants' responses to the stimulus. However, if social facilitation of responses to playbacks did occur (as seems likely), then presumably social facilitation also occurred when the elephants were responding to non-playback stimuli both before and after the playbacks. Thus, if after the playback the level of response behaviors increased over the pre-playback level, we judged that *at least* one animal had perceived the playback and scored the trial as +.

For each playback trial, an overall response score was determined by summing the +/– scores for the three response behaviors. When a trial had more + than – scores, it was given an overall score of +; when there were more – scores than +,

the overall score was  $-$ ; when there were the same number of  $+$  and  $-$  scores, the overall score was  $s$ . All behaviors were given equal weight in this comparison.

Two of the authors scored the video tapes for the occurrence of each of the three response behaviors. To control for observer bias, a naive observer, who did not know either the purpose of the experiments or that playbacks had occurred, also scored a subset of the data for the two visually observable behaviors. This subset consisted of 10 randomly selected playbacks, with each playback divided into pre- and post-playback sections. These sections were presented to the naive observer in a random order, so that data from different playbacks were intermixed and pre- and post-playback intervals did not always follow one another. This removed the bias that might be introduced if the naive observer noticed increasing responses midway through each observation period.

### Results

Table 1 presents a summary of our quantitative results. All response behaviors occurred more after the playback than before it, for both males and cow-calf groups, at both 1.2 and 2.0 km. The overall response scores indicate statistically significant (sign test,  $P < 0.02$ ) responses to the playback by males and cow-calf groups at 1.2 km and by males at 2.0 km. The responses of females at 2.0 km were not statistically significant. Responses of males and cow-calf groups were both less pronounced at 2.0 km than at 1.2 km. At each distance, the elephants responded approximately equally to trials conducted early and late in the field season.

All the calls used as stimuli elicited responses from the subject elephants. Although observers on the tower occasionally heard a brief ( $< 2$  s) snatch of sound during a playback, the elephants responded equally well to playbacks which the observers did and did not perceive.

Responses to playbacks varied from trial to trial. Not all of the behaviors quantified in Table 1 were present in every trial, and responses often included other behaviors in addition to those listed in the table. In a full response, one or more animals would lift their heads within a few seconds of the onset of the playback and raise, spread and stiffen their ears, and then freeze, apparently listening. Simultaneously or shortly after this, one or more animals vocalized. The animals would then 'scan', slowly swinging their heads from side to side, orient towards and move towards the loudspeaker. Each of these responses occurred substantially more often just after than just before the playbacks. The responses not included in the table were those that were difficult to quantify, especially on tape recordings that showed large groups or had been recorded in moonlight, and so were omitted from our quantitative analysis.

The responses of males and cow-calf groups to playbacks were often somewhat different. Animals in cow-calf groups tended to give vocal responses more than animals in all-male groups. Male responses tended to persist longer and to involve movement over longer distances than did those of cow-calf groups. In three of the eight times that the estrous call (stimulus 1) was presented to males at 1.2 km,

Table 1. *A summary of the responses of elephants to the playback of conspecific low-frequency calls, as scored by knowledgeable observers*

Distance	Target group	Response behavior			Overall score
		Vocalizing	Freezing	Moving	
1.2 km	Males	2+	10+	11+	13+
		0-	0-	1-	0-
		6s	5s	4s	3s
		N=8	N=15	N=16	N=16
		P=0.50	P<0.01	P<0.01	P<0.01
	Cow-calf groups	5+	5+	4+	10+
		0-	0-	2-	0-
		1s	1s	0s	0s
		N=6	N=6	N=6	N=10
		P<0.06	P<0.06	P<0.65	P<0.01
2.0 km	Males	1+	5+	6+	9+
		0-	0-	1-	1-
		0s	5s	4s	1s
		N=1	N=10	N=11	N=11
		P≈1.00	P<0.06	P<0.12	P<0.02
	Cow-calf groups		2+	3+	4+
			0-	2-	2-
			2s	4s	3s
		N=0	N=4	N=9	N=9
			P=0.50	P≈1.00	P<0.69

Entries indicate number of trials in which each of three response behaviors increased (+), decreased (-) or remained the same (s) after the playback. An 'overall score' is also given for each trial (see text).  
*N*=number of playbacks where the recording was adequate to score the behavior.  
*P*=probabilities determined by sign test (two-tailed).

the males walked very straight courses for 1 km or more in the direction of the playback, in two cases passing within 100 m of the loudspeaker and continuing onwards in the same direction. In each of these cases, the courses followed by the elephants did not entirely coincide with any of the well-worn trails that were almost always used by elephants approaching and leaving the area of the waterhole. The course chosen by the animals was highly unlikely to have occurred by chance, as in over 400 h of observation elephants never passed this close to the loudspeaker in the absence of playbacks. During this behavior the males walked steadily, pausing periodically to freeze and scan with ears stiffened and spread. The trunk was sometimes raised in an S-curve and slowly swung left and right, as if searching for some olfactory cue.

Movements of cow-calf groups towards the loudspeaker were not as persistent as those of males, and typically ended in dustbathing or drinking within 100 m of the start of the movement.

It is important in interpreting these results, however, to note that the playback stimuli used for males and females were not equivalent, so that we cannot, on the basis of these experiments, attribute these differences solely to the difference in the sex of the respondents.

The naive observer saw equal or greater responses to the playbacks than those seen by the knowledgeable observers 95 % of the time, with an 84 % rate of complete agreement. In all cases the greater response seen by the naive observer was when she scored a trial as + when the knowledgeable observers had scored it as s. The only time that the naive observer failed to see a response seen by the knowledgeable observers was on one occasion when the light was very low and the naive observer judged the behavior to be unscorable.

### Discussion

The effort to document responses to distant stimuli is fraught with difficulties, which in the present study were compounded by the fact that the signals we wished to study are largely below the range of human hearing. Therefore, we limited ourselves to a very simple objective – to document response or non-response, without attempting to differentiate between different sorts of responses to different calls.

We directly observed elephant responses to playback stimuli from distances of 1.2 and 2 km. However, for two reasons these are almost certainly underestimates of the distance at which elephants can perceive each other's calls. First, our playback stimuli were broadcast at only half the amplitude (i.e. -6 dB) of the strongest calls in our sample, a procedure made necessary by the limitations of our loudspeaker. Sound at the frequencies of the playback stimuli is predicted to propagate with essentially no attenuation in excess of the 6 dB loss per doubling of distance that results from spherical spreading of the sound energy (Ingard, 1953; Beranek, 1971). The 6 dB reduction (relative to actual elephant calls) that we imposed on our broadcast stimuli thus corresponds to a halving of the effective broadcast distance, so we estimate by extrapolation that the strongest elephant calls are audible to conspecifics at least 4 km away.

Second, while it was possible to demonstrate perception on the basis of the presence of certain visible and acoustic behaviors, their absence did not necessarily indicate non-perception. It is unlikely that any animal will respond overtly every time it perceives a conspecific call, and distant calls on the whole probably evoke fewer and less immediate behavioral changes than nearby calls. We suspect, therefore, that more elephants perceived more stimuli than we documented, and that elephants are less likely to respond overtly to a perceived call with increasing distance – again leading to a conservative estimate of audible range.

An alternative paradigm for estimating the 'active space', or audible distance, of bioacoustic signals is to perform calculations based on the source intensity and transmission properties of the signal and on the auditory threshold and masking functions of the listener's ear (e.g. Marten and Marler, 1977; Brenowitz, 1982).

These calculations provide no direct evidence about an animal's ability to perceive a signal, but allow the outside limits of this ability to be inferred from other information. Our experiments, in contrast, provide some direct knowledge of the range within which elephant calls function, but they do not provide an outside limit. It is not yet possible to calculate the theoretical audible limit for elephants, since some of the basic measurements (e.g. auditory thresholds and masking functions in the African elephant) are unknown.

Although our sample size of responses to particular calls is too small to permit a statistically valid discrimination between the functions of the calls, we observed conspicuous differences between male and female response behaviors which seem worthy of comment. The tendency for cow-calf groups to vocalize more than males, and for males to make longer movements towards the loudspeaker than females, may reflect different strategies that are adaptively appropriate. The tendency of elephants in cow-calf groups to vocalize in response to the calls of distant elephants may help to coordinate movements of separated groups by informing distant groups of the presence and location of the caller's group, and by alerting members of an elephant's own group to the fact that other elephants are within hearing distance. The tendency of males, in contrast, to respond to distant calls by silently and quickly moving in the direction of the source may reflect a strategy that improves a male's chances of locating a potential mate before she is found by competing males. Inter-male competition is likely to be a relevant consideration in our experiments because 93 % of the playback calls we used for males were calls associated with reproduction. When a male elephant perceives a call that could indicate a receptive female, it may be to his advantage to remain silent so as not to alert rivals (Poole, 1987), and to move towards the source of the call as quickly as possible.

The function of different call types remains to be investigated further, since our experiments were not designed to distinguish between calls, but rather to provide an indication of their audible range. Our results support the hypothesis that the low-frequency calls of elephants function in communication among elephants over distances of several kilometers.

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