



Signals and assessment in African elephants: evidence from playback experiments

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A series of playback experiments using two elephant vocalizations, the 'musth rumble' and the 'oestrous call', was carried out in Amboseli National Park to examine signalling and assessment in African elephants, *Loxodonta africana*. In response to the musth rumble of a high-ranking male other musth males approached the speaker aggressively, whereas nonmusth males walked away from the stimulus. The call of an oestrous female, too, attracted musth males who approached the speaker rapidly, while nonmusth males listened and then walked away. Females listened and often showed considerable interest in the musth rumbles of males, approaching the speaker and sometimes responding by vocalizing and/or secreting from the temporal glands. The experiments bear out earlier observational data and game theory predictions which suggest that by being in or out of musth a male may be conveying information about the relative value he places on contesting his dominance rank and his access to oestrous females. When not visibly in musth, a male may be indicating his intention not to contest access to oestrous females.

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Assessment theory (Parker 1974; Maynard Smith & Parker 1976) predicts that selection should favour individuals who are able to assess the physical and behavioural traits of rival males and, with this knowledge, adjust their own behaviour to the costs and benefits of fighting and the probability of winning. In the case of mature male African elephants, *Loxodonta africana*, who exhibit strong sexually active musth and inactive nonmusth periods, the costs and benefits of fighting may vary depending upon the time of year (Poole 1989a). Earlier work (Poole 1989a) suggested that the heightened sexual and aggressive period of musth may be an example where the value a male places on gaining access to receptive females varies with time and is correlated with a physiological condition and announced by means of reliable signals that allow individuals to assess whether they should engage or retreat (see Parker & Rubenstein 1981). During musth, males announce their sexual and aggressive state with powerful pulsed infrasonic calls, temporal gland secretion and urine dribbling. Like signals in some other animals (e.g. Ryan 1988; Prestwich 1994), some of these signals are costly (high-ranking males lose a median 345 litres per 24 h; Poole 1989a) and, thus, difficult to fake (Zahavi 1977; see also Enquist 1985; Johnstone & Grafen 1992). Musth is energetically expensive and by the end of musth males have lost considerable condition (Poole

1989a). During nonmusth, males spend much of their time feeding, resting and regaining strength (Poole 1987). Bulls may be willing to engage in such competitions during their annual musth only when they are in peak condition. In an earlier paper (Poole 1989a) I argued that, during musth, males are signalling a willingness to engage other males for access to oestrous females, whereas nonmusth males, no matter how large or high ranking, are signalling that they have no intention of contesting access to oestrous females.

To test this hypothesis, playback experiments were designed to examine the responses of mature musth and nonmusth males to the presence of a musth male and to the presence of a receptive female. To simulate the presence of a musth male, I used a stimulus of a call made only by males during their musth period, the 'musth rumble', and I simulated the presence of an oestrous female by using a stimulus of a vocalization, the 'oestrous call', made only by females in oestrus.

The patterns of musth and the behaviour of musth males have been described in detail elsewhere (Poole 1987, 1989a, b; Hall-Martin 1987; Poole & Moss 1989) and only a summary is presented here. As adult male elephants continue to grow in height and weight, older males are generally dominant to younger ones (Poole 1989a). Males produce sperm in quantity by ca. 17 years old (Laws 1969), but at this age they are only half the weight of a large adult male (Laws 1966). Although young males show interest in oestrous females they have very

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limited opportunities for mating, owing to the intense competition from older males (Poole 1989a) and strong female preference for these mature individuals (Moss 1983; Poole 1989b). By 25 years old, males have begun annual sexual cycles, spending a few months each year in the company of female groups and a greater portion of the year in the company of other males (Poole 1987). By 30 years old, the majority of males have experienced their first musth which occurs at some point within their sexually active period. During musth, male elephants experience dramatic surges of circulating testosterone (Hall-Martin & Van der Walt 1984; Poole et al. 1984); they interact aggressively with other large adult males, particularly those in musth, and spend much of their time searching for, attempting to gain access to, or guarding oestrous females (Poole 1987, 1989a, b; Poole & Moss 1989). Musth is characterized by a distinct posture, swollen and secreting temporal glands, dribbling of strong-smelling urine, and a particular, very-low-frequency, vocalization, the 'musth rumble' (Poole 1987; Poole et al. 1988). Among males 20–30 years old, musth typically lasts several days to perhaps a week at a time, and may occur several times during the sexually active period. Musth usually lasts several weeks in males 30–35 years old, 1–2 months in males 35–40 years old and 2–4 months in older males (Poole 1987). In general, males with longer musth periods lose more condition than those males with shorter periods (Poole 1989a). Musth periods are asynchronous and each male is on his own particular cycle (Poole 1987).

Musth has a dramatic effect on the relative dominance ranks of males (see Poole 1989a); with few exceptions, a musth male, whether large or small, ranks above all nonmusth males. Since the musth periods of males are asynchronous, small sexually active musth males may meet and interact with larger, sexually inactive non-musth males. Between two musth males, dominance is usually based on body size although there are exceptions to this rule. Again, because musth periods are asynchronous, a large male in poor condition towards the end of his musth period may meet a smaller male in peak condition at the beginning of his period. Asymmetries between body size and condition lead to the majority of serious fights. Escalated contests also occur between males who are closely matched in both size and condition. Musth males interact aggressively whenever they meet, and the presence of an oestrous female is not a prerequisite for a fight.

To investigate the response of musth and nonmusth males to the presence of a musth male and an oestrous female, I used two vocalizations, the musth rumble and the oestrous call, respectively (the oestrous call is described in Poole et al. 1988 as the 'postcopulatory sequence'). I also examined how females respond to the calls of a high-ranking and a low-ranking male. Without the availability of field data we might expect all mature males to approach the sound of a receptive female and perhaps for large males to approach the sound of an aggressive male and smaller males to move away. Based on field observations and game theory predictions, however, we expect radically different behaviour. Sexually

active musth males should move towards both calls, while sexually inactive nonmusth males should move away from the sound of a musth male and they should also avoid the vocalization of an oestrous female since the call suggests the likely presence of a male in musth (Poole 1989a, b).

METHODS

Study Area

I carried out playbacks on a population of free-ranging African elephants in Amboseli National Park, southern Kenya, from January 1988 to May 1990. Previously, I had undertaken a long-term study of musth on the same population from 1976 to 1988 (see Poole 1987, 1989a, b). Amboseli National Park and the surrounding area is inhabited by a population of elephants currently numbering ca. 1000 individuals, including 50 matriarchal families and some 190 adult males. The elephant population has been under continuous study since 1972. All elephants are known individually and are habituated to vehicles. The Amboseli ecosystem consists of semiarid wooded, bushed and open grasslands interspersed with a series of permanent swamps. Rain falls in two distinct seasons and averages 350 mm/year. The area used by the majority of elephants during the daytime is primarily open grassland and swamp edge grassland.

Playback Stimuli

Elephants produce over 27 different very-low-frequency calls known as rumbles (unpublished data; see also Poole et al. 1988). Two of these calls were used in this study: the musth rumble and the oestrous call.

The musth rumble is a distinctive call that is qualitatively different from all other elephant rumbles. A key feature of the musth rumble is the repeated pulsations that appear to resonate in the nasal passages of the skull and upper trunk and overlay the harmonic frequencies. Since males produce this call only when they are in musth, the call is a reliable indication of the presence of a musth male. Lone musth males rumble with the highest frequency, and musth males in the company of females rumble more often than those guarding an oestrous female do. Females sometimes respond to musth rumbles by calling in unison with a 'female chorus' (Poole et al. 1988; Poole & Moss 1989), by secreting from the temporal glands and by urinating and defecating.

The musth rumble (Fig. 1a) has a fundamental frequency that starts at a median frequency of 12 Hz (interquartile range 11–14, $N=76$), rises to a median of 17 Hz (interquartile range 16–19 Hz, $N=80$) and falls to a median frequency of 11 Hz (interquartile range 10–12 Hz, $N=78$). The median duration of the musth rumble (excluding the pulsations that typically precede the harmonics) is 4.4 s (interquartile range 3.8–4.9 s, range 2.5–7.5 s; $N=78$). The musth rumble has a median sound pressure level of 92 ± 3 at 1 m (interquartile range 90–93, $N=62$).

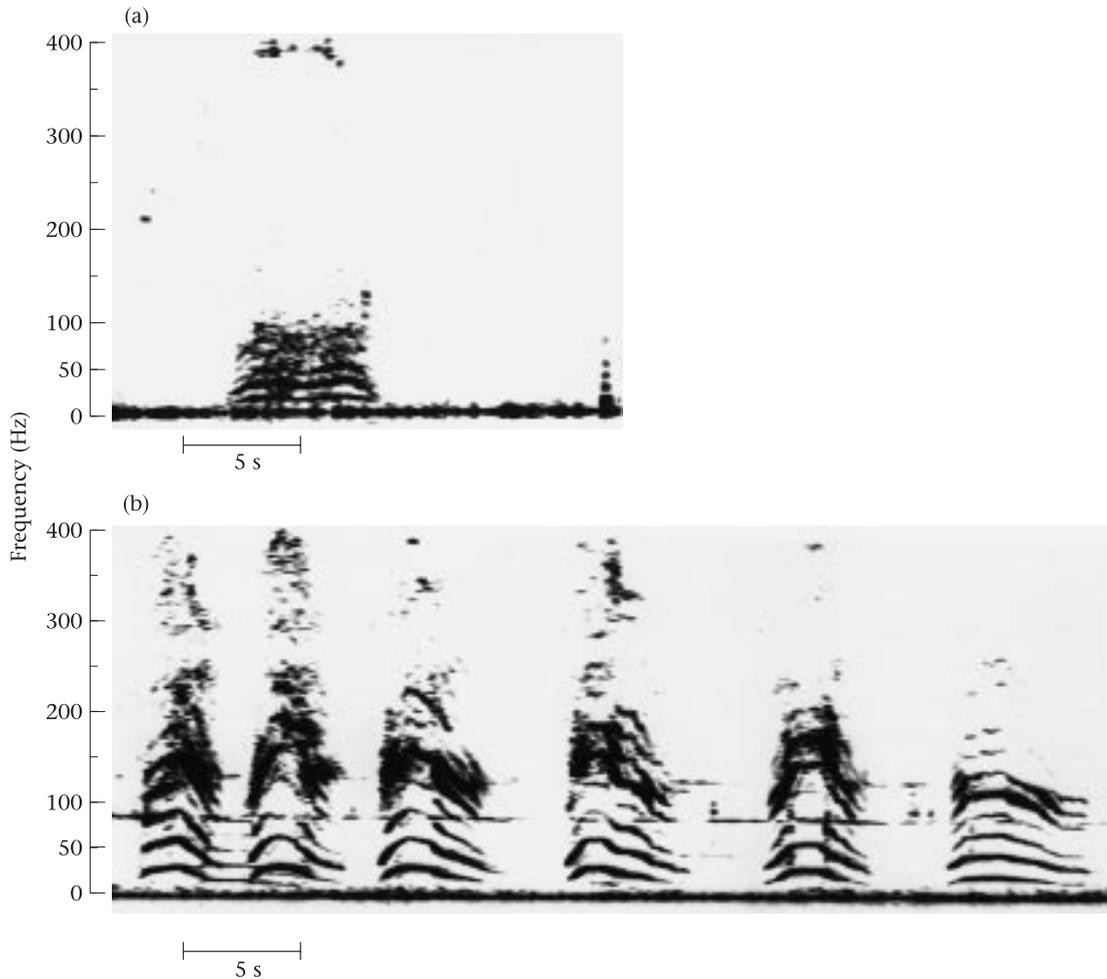


Figure 1. Spectrograms of (a) a musth rumble and (b) an oestrous call.

The musth rumble stimulus that I used for playbacks to other males, from male 119, started with a fundamental frequency of 14 Hz rising to 18 Hz and ending at 12 Hz. It lasted 3.4 s and its sound pressure level was 91 ± 3 at 1 m. For the playbacks to females, I used both this stimulus and one recorded from a lower-ranking male, M12. The latter stimulus started with a fundamental frequency of 12 Hz, rising to, and ending at, 12.5 Hz; it lasted 5.0 s.

The oestrous call is also a very distinctive rumble given only by females in oestrus and usually, although not always, immediately after a mating (Fig. 1b). The rumble is repeated as a sequence of highly modulated calls and calling may last anywhere from several seconds up to 45 min (unpublished data). The fundamental frequency of the oestrous rumble (Fig. 1b) starts at a median of 17 Hz (interquartile range 17–17, $N=14$) rising to a median of 26 Hz (interquartile range 24–29 Hz, $N=15$) and falls to a median frequency of 16 Hz (interquartile range 15–16 Hz, $N=15$). The median duration of one rumble is 5.0 s (interquartile range 4.4–6.0 s, range 3.1–6.8 s, $N=13$). The sound pressure level of this rumble varies, beginning at around 115 dB at 1 m from the source (extrapolated from 96 dB at 10 m; Poole et al. 1988) and declining as calling continues.

The oestrous call that I used consisted of a sequence of four rumbles. Each of the four rumbles started with a fundamental frequency of 17 Hz and ended at 16 Hz. They rose in mid-call to 26, 25, 22 and 24 Hz, respectively. The entire sequence lasted 37 s.

Equipment

Many elephant rumbles are produced at high sound pressure levels and all rumble-type calls contain components at or below the level of human hearing (Poole et al. 1988; unpublished data). The sound equipment used in these experiments was capable of recording/producing sounds down to 10 Hz. Elephant vocalizations were recorded on a Nagra IVSJ, using two MKH 110 Sennheiser microphones. The Nagra's low-frequency response is very uniform between 20 Hz and 1 kHz, but the response starts to fall off below 20 Hz. It is down -1.5 dB at 15 Hz. Additionally there is a minor dip (-0.5 dB) at 60 Hz and a small rise ($+0.5$ dB) at 80 Hz. By making use of the FM track, however, the Nagra had a lower limiting frequency of 2.5 Hz. I played back particular calls to the elephants through the Nagra tape recorder, using a 300-W/channel Zues amplifier (frequency

response at 1 W=2 Hz–200 kHz, 3.0 dB) and a 200 LB speaker. The speaker was custom designed by Intersonics Inc. (Northbrook, Illinois, U.S.A.) and was equipped with two 18-inch motor-driven woofers and four passive radiators. A second smaller speaker also equipped with an 18-inch woofer was used to produce the higher frequency components of the calls. Prior to use in the field, the playback system was tested (by D. Wickstrom) and found capable of a flat response down to 10 Hz.

Sound pressure levels of the stimuli were calibrated using a Realistic Sound Pressure Level Meter to conform with natural levels (80 dB re 20 μ Pa and 102 dB re 20 μ Pa at 5 m from the source for the musth rumble and the oestrous call, respectively). The Realistic meter has a flat response between 20 and 1500 Hz.

All playback experiments were filmed with a Sony video camera. In addition, I recorded the playback experiments on audiotape, with a custom-designed 'infrasound translator', a device that translated low-frequency sounds into an audible range so that I could detect any vocal responses of the elephants even if they were inaudible.

Playback Protocol

Elephants have a marked ability to localize low-frequency sound (Heffner & Heffner 1982), and thus I believed that it was important to ensure that the speaker was both some distance from the subject and hidden from his/her view. In other words, if the elephant walked in the direction of the stimulus and eventually stopped next to the speaker, it would have been conceivable that an elephant had been there, behind that bush, several minutes beforehand. Even though elephants sometimes responded by walking 100 m and stopping near or next to the speaker car, they would be unlikely to associate the sound with the car since they were used to the presence of the car and its occupants even when no sounds were heard.

Since the speaker was in a vehicle hidden from view, I placed myself with a video camera in a second car in a position where I could monitor both the subject(s) and the speaker car. The aim was to have the speaker car at least 100 m away from the subject for the playback of the oestrous call stimulus and 60 m away from the subject(s) for playbacks involving a musth rumble. Owing to the rather sparse vegetation, these exact distances were not always possible. The mean distance \pm SD to subjects during the oestrous call experiment was to musth males 105 ± 14 m (range 90–130 m, $N=9$) and to nonmusth males 100 ± 9.5 m (range 85–120 m, $N=10$). The mean distance \pm SD to subjects in the musth rumble experiments was to musth males 75 ± 19 m (range 50–110, $N=10$), to nonmusth males 67 ± 21 m (range 30–100 m, $N=8$) and to female groups 64 ± 21 m (range 35–100 m, $N=15$).

When a group containing a potential male subject was situated in a suitable location, a particular individual was selected beforehand as the focus of the playback. While the behaviour of the group in general, and interesting behaviour of any individual, was noted, the results are based only on the selected subject's response. The

experiment involving playbacks to females was scored differently. Since the behaviour of family groups is much more interdependent, the results of playbacks involving families include the responses of all adult females (see below).

I initiated experiments when the subject was either stationary or moving perpendicular to the speaker, but never when the subject was moving towards or away from the speaker. The playback system took approximately 4 min to set up and my assistants signalled to me when they were ready. I signalled back to them as I began filming, whereupon they timed 1 min and then played the stimulus call once. I continued to film until the subject returned to his or her previous activity or had disappeared from view.

I specifically decided not to match pairs for two reasons: first, because of the difficulty of locating and completing a playback on a particular male both in and out of musth and second because of the possibility that it might have affected the male's response. Males therefore contributed to an experiment as either a musth or as a nonmusth male subject.

Based on personal observation, I assumed that males might be able to identify the musth rumble stimulus as belonging to male 119 and, therefore, that different responses might be expected depending upon the rank of the subject male relative to male 119. I already knew from observational data that musth has a dramatic effect on rank, and musth males are dominant to all nonmusth males regardless of size. To demonstrate the strength of this phenomenon I attempted to weight the musth rumble experiments with musth male subjects who were smaller than male 119 (8/10) and nonmusth male subjects who were larger (5/8).

Pseudoreplication and Sample Size

In early 1985, African elephants were discovered to produce vocalizations at high sound pressure levels containing components well below the level of human hearing (Poole et al. 1988). In 1986–1987 when the stimulus recordings were made, and in 1988 when the experiments were undertaken, playbacks involving elephant vocalizations presented a particular challenge. In addition to the difficulty of carrying out playback experiments involving large and highly mobile animals, there were numerous technical and logistical problems to overcome. These limited the design of the experiments and led to two problems: pseudoreplication (Kroodsma 1989) and small sample size.

Pseudoreplication

In the musth rumble playbacks to males and in the oestrous call playbacks, I used only a single stimulus. During the early stage of the study I had difficulty obtaining a sufficient number of high-quality recordings. Also, owing to the particular specifications and expense of the equipment, making playback stimulus tapes in Kenya was impossible. Thus once the original stimuli were made at Cornell in 1987 I was limited to those for my experiments.

Although I had musth rumbles from several males, there were additional reasons for using only one stimulus for the musth rumble playbacks to males. Earlier work (Poole 1987) showed that musth males rumble under a variety of different specific circumstances (e.g. when drinking, listening, mud splashing, marking, threatening, during fights and when approaching a new group of females). Considerable acoustic variation appeared to exist not only between the musth rumbles of different males, but also between those made by a single musth male. I postulated that these differences might reflect specific acoustic information (Poole 1987).

To minimize any potential confounding of the results by using stimuli of males of different rank, or to avoid using acoustically different musth rumbles, thus possibly introducing different information from different males, I selected one high-quality recording, from male 119, and used it throughout.

When a female is mated, her oestrous call is usually overlaid by the rumbles, roars, screams and trumpets of other family members in what is called a 'mating pandemonium' (Poole et al. 1988). Shirley's oestrous call was the only 'clean' vocalization available to me at the time. Of note is that a second oestrous call recorded in Amboseli by K. Payne and played back to elephants in Namibia succeeded in attracting males from several kilometres away (Langbauer et al. 1991).

Although these experiments suffer from pseudo-replication in the use of one stimulus, the robust and consistent responses of the elephants as well as the results of the acoustic analysis make it unlikely that the calls used are odd or deviant. At this stage the strong differences between the reactions of musth and nonmusth males are presented to gain further insights, and to look at the individual response to the presentation of an identical call.

In the final experiment in which a musth rumble was played to different family groups, two musth rumbles were used, one from male 119 and one from male 12. I knew from observation that females respond to the arrival of a musth male with considerable excitement and I simply wanted to know whether the sound of a musth rumble was enough to elicit a similar response.

Sample size

Given the logistical difficulties of carrying out each playback, I was aware early on that sample sizes would be limited. In addition, the scheduling of field trips and the timing of different males' musth periods also affected the availability of subjects as described below.

Playbacks were carried out during 8 months over 3 years (during July, August, September and December 1988; April, September and December 1989; March 1990). During these 8 months, 25 different males were observed in musth out of a possible 46 who were old enough and known to come into musth between January 1988 and May 1990. Of these 25 available musth males, nine were subjects in the oestrous call experiments and 10 were subjects in the musth rumble experiments (Table 1). Five of these musth males, 78, 131, 135, 175 and 201, were subjects in both the musth rumble and the oestrous call

Table 1. The number of days that subject males were observed in musth during the months that playbacks were undertaken in 1988, 1989 and 1990, and the experiments that they contributed to as musth (M) and/or nonmusth (NM) males

Male	Days observed in musth	Musth rumble experiment	Oestrous call experiment
5	6	M	
7	1		NM
10	1	NM	NM
13	6	NM	NM
22	6	M, NM	NM
41	0	NM	NM
45	1		NM
51	1		NM
57	3	NM	
78	7	M	M
80	0	NM	
91	2		M
93	0		NM
97	0		NM
114	0	NM	
115	1	M	
119	1		M
125	1	M	
126	8		M
131	5	M	M
132	0		NM
135	2	M	M
145	1	NM	
159	1	M	
174	1		M
175	3	M	M
201	4	M	M

experiments. In all, 14 musth males and 14 nonmusth males were used. Table 1 summarizes the males observed in musth during the 8 months of experimental work and the number of days each was sighted in musth during these months.

Since the musth period of male 119 typically lasted only 3 months (June, July and August) and since only a few other males came into musth during the same period, carrying out playbacks when he was in musth would have limited the sample size even further. Playbacks involving the musth rumble stimulus were, therefore, undertaken only when male 119 was not in musth, starting from September 1988. Except on one occasion, male 119 was never in the vicinity when the call was played.

During the oestrous call experiments a stimulus from female Shirley was used. I carried out 19 playbacks, nine to males while in their musth and 10 to males out of musth (Table 1). During the musth rumble experiment, a musth rumble stimulus recorded from male 119 was used in 18 playbacks. Ten playbacks were presented to males in musth and eight to males out of musth (Table 1).

In the final experiment, 15 playbacks were undertaken. The musth rumble from male 119 was played to six families and that from male 12 was also played to nine families.

Group size

Owing to the fluid nature of elephant society, it was not possible to control for the size and composition of

groups receiving playbacks, and subjects might be found alone, in an all-male group, in association with a group of females, or in a mixed group. While members of a family group typically responded to a stimulus as a unit (with members usually following the matriarch's lead), males tended to give an individual contextual response. In addition, even if there might have been some social facilitation effect, the musth to nonmusth male comparisons in each experiment both include a range of group sizes and compositions.

During the oestrous call experiment, musth male subjects were alone on three occasions, with other males on five occasions and once in a mixed group. Group size ranged from one to 80 individuals. During the same experiment, nonmusth male subjects were alone during two playbacks, and with other males on eight occasions. Group sizes ranged from one to 35 individuals. During the musth rumble experiment, musth male subjects were alone three times, with families on three occasions, and in mixed groups on four occasions. Group sizes ranged from one to 40 individuals. Nonmusth subjects were alone four times and with other males four times. Group size ranged from one to 12 individuals. During the experiment where musth rumbles were played to 15 family units, these groups ranged in size from two to six adult females.

Male Rank

Table 2 shows the dominance ranks of subject males, each male's estimated year of birth (± 3 years) and the approximate duration of his annual musth period during the late 1980s.

Description of Behaviours

The behaviours described below occur in a variety of situations; they are not anomalous postures and behaviours merely associated with the playback stimuli. Many of these behaviours have already been described (e.g. Poole 1987, 1989a; Poole et al. 1988; M. P. Kahl, personal communication).

(1) Aggressive behaviour: walking or standing with the head raised well above the shoulder with the jaw 'tucked in'; folding the lower half of the ears back so that a prominent ridge appears across the ear; increasing the rate of urine dribbling; musth rumbling. Any combination of these behaviours was scored as aggressive behaviour.

(2) Apprehensive behaviour, as defined shortly, usually precedes fleeing or escape responses. Elephants show very distinct posture and behaviour when they are apprehensive or alarmed. These include: standing with the head raised with the jaw extended outwards; holding the ears raised and stiffened; twitching the tip of the trunk back and forth; reaching up with the trunk to touch the temporal gland, the side of the face or the lip; turning a raised head from side to side with the trunk curled under; turning away or walking away while looking back over the shoulder; raising one foreleg as if with intention of

Table 2. Dominance rank order, year of birth and approximate duration (number of weeks/year) of musth of subject males

Male	Rank	Birth year	Musth duration
13	1	1935	5
126	2	1939	10
22	3	1940	14
41	4	1935	Not seen in musth
78	5	1945	17
80	6	1945	8
7	7	1945	12
119	8	1947	11
45	9	1945	12
10	10	1945	10
51	11	1946	14
114	12	1950	10
97	13	1952	5
57	14	1950	5
175	15	1948	9
174	16	1953	6
125	17	1953	9
91	18	1951	8
145	19	1953	8
132	20	1953	4
131	21	1953	4
5	22	1956	5
12	23	1956	3
93	24	1957	5
135	25	1957	4
201	26	1960	6
159	27	1961	3
115	28	1962	2

departure; raising the tail. Any combination of these postures was scored as apprehensive behaviour.

(3) Listening: an elephant seldom stands stock still except when listening or resting; usually some part of the body, ears, trunk, tail, etc., is in motion. When resting, an elephant relaxes its head and ears usually allowing its head to hang below its shoulders and its ears to flop forward. A listening elephant, on the other hand, stands with its head raised and its ears lifted and slightly extended and may slowly turn its head to the left and right as if trying to localize a sound. Elephants are very accurate (to within 1° for broadband noise) at sound localization (Heffner & Heffner 1982).

(4) Rumble: a low-frequency vocalization. In the case of musth males these were all musth rumbles. Females usually responded to a musth rumble with a 'female chorus', a particular vocalization made by females upon the arrival of a musth male (Poole et al. 1988).

(5) Smelling: olfactory signals play an important role in mutual recognition and communication between elephants (Brown 1985). Aside from urine and faeces, elephants produce odorous secretions from their temporal glands, tarsal glands and interdigital glands. The tip of the trunk is almost never stationary, moving in the direction that the elephant appears to find interesting. When attempting to gain more information about the location of a conspecific, an elephant may raise its trunk high in the air, like a periscope, or may snake the trunk back and forth along the ground as it searches for or

Table 3. Percentage of playbacks during which specific behaviours were observed when the oestrous call stimulus or musth rumble stimulus was played to musth and nonmusth males

	Oestrous call		Musth rumble	
	Musth N=9	Nonmusth N=10	Musth N=10	Nonmusth N=8
Listens to stimulus	100	100	100	100
Walks away	0	60	0	62
Orients towards speaker	89	50	100	87
Walks towards speaker	89	30	100	12
Apprehensive behaviour	0	70	20	62
Aggressive behaviour	0	0	50	0
Smells in direction of speaker	78	40	100	87
Vocalizes	33	0	0	12

follows the trail of the other elephant. Musth males frequently use these techniques to track other musth males and to search for oestrous females (personal observation) and both were scored as smelling.

(6) Temporal gland secretion: the onset of secretion from the temporal glands. This was scored in the playbacks to females only. Female African elephants secrete under a variety of circumstances, but most noticeably when they are socially excited. Temporal gland secretion is very commonly associated with the female chorus (see 4 above).

(7) Urination: urinates. This was scored in the playbacks to females only. Females frequently urinate when they are approached and/or tested by a musth male.

In addition, I recorded whether an elephant oriented towards or away from the speaker (i.e. turned to face it or away from it) and walked towards or away from it.

RESULTS

Oestrous Call to Musth and Nonmusth Males

When I played back the oestrous female call to large adult males who were either in or out of their musth period, all subjects stopped what they were doing and listened, but thereafter musth males (N=9) and non-musth males (N=10) behaved quite differently (Table 3). Musth males approached the stimulus rapidly, while nonmusth males walked away from it ($\chi^2_1=9.7, P<0.01$). Nonmusth males also displayed considerable apprehensive behaviour at the sound of the oestrous call, while musth males did not ($\chi^2_1=10.9, P<0.001$).

Musth Rumble to Musth and Nonmusth Males

When presented with the stimulus call of a musth male (Table 3), nonmusth males moved away, even when they were larger and normally higher ranking (when neither was in musth) than the calling male (Table 4). Musth males did not move away, even when they were younger and normally (when neither was in musth) lower ranking (Table 4). Musth males typically moved towards the

speaker rapidly while nonmusth males moved away ($\chi^2_2=20.9, P<0.001$). In addition, musth males were aggressive, while nonmusth males showed apprehensive behaviour ($\chi^2_2=11.8, P<0.01$; Tables 3, 4).

Musth Rumble to Females

When I played back musth rumbles of male 119 (N=6) and the lower-ranking male 12 (N=9), all the females listened, and in 53% of the playbacks females sought additional information by continued listening combined with smelling the air with their trunks raised. In eight of the playbacks (53%) females oriented towards the speaker and in six cases (40%) they walked towards it. Although further playbacks are needed to draw any conclusions, females did respond differently to the calls of the two males. While females in all but one family walked towards the call of male 119, they approached the call of male 12 only once and in three cases actually walked away from his call ($\chi^2_2=8.5, P<0.02$; Table 5).

In a number of the playbacks females responded with vocal and/or olfactory signals: in five out of 15 playbacks females rumbled, in two playbacks females began secreting from their temporal glands, and in one case a female urinated and defecated. Again the stronger responses were elicited by the call of male 119 (Table 5).

Table 4. Percentage of playbacks during which specific behaviours were observed when the musth rumble stimulus of male 119 was played to musth and nonmusth males that were larger or smaller than male 119

	Musth		Nonmusth	
	Smaller N=8	Larger N=2	Smaller N=3	Larger N=5
Walks away	0	0	33	80
Walks towards speaker	100	100	33	0
Apprehensive behaviour	25	0	67	60
Aggressive behaviour	50	50	0	0

Table 5. Percentage of playbacks during which specific behaviours were observed when the musth rumble stimulus of a low-ranking male, 12, or a high-ranking male, 119, was played to females

	Male 12 N=9	Male 119 N=6
Listens to stimulus	100	100
Walks away	33	0
Orients towards speaker	22	100
Walks towards speaker	11	83
Smells in direction of speaker	33	83
Vocalizes	11	67
Secretes from temporal glands	0	33
Urinate	0	17

DISCUSSION

This study used two stimulus calls, the musth rumble and the oestrous call, to investigate signalling and assessment in male African elephants. Only males in the heightened sexual and aggressive state of musth make the musth rumble call and playback experiments showed that this signal alone is enough to elicit a typical response by other musth and nonmusth males. The results bear out earlier observational data and game theory predictions that during nonmusth periods male elephants, whether large or small, retreat when in the vicinity of a musth male, while musth males, whether large or small, initially challenge. Only receptive females make the oestrous call and in the playback experiments sexually inactive nonmusth males moved away from these calls while musth males approached the same calls rapidly. My results also bear out predictions that sexually inactive nonmusth males should avoid receptive females.

Why should large nonmusth males retreat from the call of a potentially younger, smaller musth male and from the calls of an oestrous female? Male elephants continue to grow (Haynes 1991; Lee & Moss 1995) and reproduce until late in life (Poole 1989a). Since reproductive success is positively correlated with age and body size, the longer a male survives, the more offspring he is likely to produce (Poole 1989b). Escalated contests frequently lead to injury or death (Hall-Martin 1987; Poole 1989a), thereby reducing future reproductive potential. Males should, therefore, send a clear signal, by not being in musth, that they will not contest rank or access to receptive females when the benefits derived from winning are relatively less than could be achieved either at a different time of year or at a later stage of life.

While the apprehensive behaviour of nonmusth males was entirely expected based on previous observations and predictions, the response of musth males to the sound of another musth male was initially somewhat surprising. Musth males approached the speaker whether they were higher or lower ranking than the caller was. While this might be expected if we assume that elephants cannot recognize one another's calls individually, this assumption seems naïve for several reasons. First, the subjects are long-lived, large-brained animals who have met and interacted with one another over a period of several

decades. Second, on the basis of many years of personal observations elephants do respond to vocalizations of other elephants as if they are able to distinguish between the calls of individuals. Finally, recent playback studies (K. McComb, personal communication) have demonstrated that elephant family groups are able to distinguish from up to a kilometre away between the calls of close and more distant associates. The musth rumbles of different males are qualitatively different and I believe it is likely that these calls carry several types of information: that the caller is in musth, the caller's identity and his location (see Heffner & Heffner 1982).

Assuming that elephants recognize one another's calls individually, is there a way to explain why smaller, lower ranking males approached the speaker? One reason may be that although age and body size are primarily responsible for determining relative fighting ability between males in musth, body condition is also a factor (Poole 1989a; see also McCullough 1969; Le Boeuf 1972; Lincoln & Guinness 1973). Competition between males for access to receptive females is intense, and males cannot afford physically to remain sexually active year round. Since the amount of weight a male loses during musth is positively correlated with the duration of his musth period, and older males stay in musth for longer, younger males regularly challenge normally higher ranking males, and sometimes engage in fights that they win (Poole 1989a). Finally, since the musth periods of males are asynchronous (Poole 1987), all musth males must constantly reassess their rank relative to every other musth male.

During the musth rumble playback experiments, after listening to the call, musth males did seek additional information about the calling male by moving towards the speaker, smelling with their trunks raised high or by tracking along the ground. By approaching the caller and smelling the air for his scent and the ground for his urine trail, a musth male may be able to gain information about the calling male's condition. This additional information may help him to assess whether he should continue to approach and challenge the other male or change tactics and retreat.

Males in musth spend much of their time searching for receptive females (Poole & Moss 1989). A second reason why small musth males may approach the call of a larger male is that one method of locating females might be to approach the call of another musth male since, as additional playbacks demonstrated, females may be moving towards the call as well. Females frequently responded to the sound of a musth rumble by moving towards the speaker vocalizing, secreting from the temporal glands and urinating, all actions that might reduce the time a male spent searching for a receptive female.

Fights between musth males occur most often when there are asymmetries between relative body size and condition (Poole 1989a). While winning a fight may improve a male's future access to oestrous females, fighting carries grave risks. By being in the state of musth with its associated reliable signals, males send a very clear message that they place a high value on oestrous females, and that they intend to challenge if further assessment suggests that they have a good chance of winning. By not

being in musth, males are sending an equally strong signal that they are not willing at that time to contest access to oestrous females.

The conclusions of the playback experiments are limited somewhat owing to the small sample sizes and pseudoreplication (Kroodsmma 1989); nevertheless the robust and consistent responses do support earlier long-term behavioural observations of musth and nonmusth males and add a specifically vocal dimension to what is already known. In addition, while a single stimulus was used in the first two experiments, the point is that males responded dramatically differently to an identical call simply according to whether or not they were in musth.

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