Announcing intent: the aggressive state of musth in African elephants

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Abstract. Predictions derived from game theory suggest that animals should not signal their intentions during conflict situations. However, during the period of musth, male elephants, *Loxodonta africana*, announce a state of heightened aggression with signals that are unbluffable. Since smaller musth males in poor condition are able to dominate larger, normally higher-ranking, non-musth males in good condition, musth provides a useful system with which to examine the possibility of honest signalling of motivation, rather than of fighting ability. Despite the highly aggressive state of males in musth, escalated contests are extremely rare. The behaviour of musth and non-musth males suggests that opponents are able to estimate their often rapidly changing roles in the asymmetries with relative accuracy. Since, unlike most other rutting mammals, elephants have asynchronous sexually active periods, resource value varies both with age and the fluctuating sexual state of a particular individual. It is suggested that musth may be a case where information about resource value is conveyed.

Studies of animal communication have often assumed that signals are an expression of the signaller's motivational state. In other words, signals may express a state of aggression, fear, excitement or pain, thereby informing the receiver of the signal that the sender is likely to engage in certain forms of behaviour, such as to flee or to attack (e.g. Cullen 1966; Lorenz 1966; Smith 1966; but see Hinde 1981 and Caryl 1982).

Recently these views have been challenged by the predictions derived from game theory (e.g. Maynard Smith & Price 1973; Maynard Smith 1974; Parker 1974; Maynard Smith & Parker 1976). These predictions suggest that although selection will favour and maintain the effectiveness of signals that convey information about fighting ability, (or resource holding potential: size, weaponry, etc.; Parker 1974), which might influence the outcome of an escalated contest, signals which convey information about motivation (i.e. what an individual will do next in a given situation) will quickly lose their effectiveness (Andersson 1980). Difficulties arise in accounting for the transfer of information about intentions because it is hard to see what would prevent an animal from lying. In other words, if simply announcing, 'I am going to attack you' wins contests whether or not the individual intends, or is able, to do so, then cheaters would have a selective advantage. Soon most members of the population

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would signal false aggression and announcement would become meaningless. However, there are examples of animal conflicts where individuals do appear to signal aggressive intent.

In a discussion of aggressive commitment in animal conflicts, Maynard Smith (1982) cited the phenomenon of musth in male African elephants, *Loxodonta africana* (Poole & Moss 1981) as one such example. During the period of musth, male elephants anounce a state of heightened aggression and intention to fight with glandular secretions and by urine-marking and vocalizing (Poole 1987). Maynard Smith argued that commitment to aggressive behaviour requires a prior asymmetry. For example, one player might be larger and therefore able to commit himself to the best course of action in that situation (which could be aggression) no matter what the other contestant chooses to do. Maynard Smith (1982) pointed out that the commitment must be announced and, once announced, it must be irrevocable.

The behaviour of elephants, and of other species (e.g. Pere David's deer, *Elaphurus davidianus*: Wemmer et al. 1983; red deer, *Cervus elaphus*: Walther 1984; see below), however, suggests that announcement of aggressive intent is sometimes revocable and that some more subtle signal is being conveyed. 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 elephants, the costs and benefits of escalation for a particular male with another may be a very time-specific value and Parker & Rubenstein (1981) describe a situation in animal conflicts which might apply: where there is an interaction between two asymmetries, such as fighting ability and resource value, and opponents sustain costs (K) at rates K_A and K_B and their values of winning (V) are V_A and V_B, then a unique evolutionarily stable strategy exists of the rule 'fight on estimating role A, where $V_A/K_A > V_B/K_B$; retreat if B'. Parker & Rubenstein (1981) suggested that accurate assessment of relative resource holding potential, or fighting ability, might be possible (e.g. Geist 1971; Davies & Halliday 1978; Clutton-Brock & Albon 1979), but that estimates of V_A and V_B might be difficult, particularly if correlated with some physiological condition, rather than with ownership.

Musth in elephants may be an example where signallers convey information about relative resource value. Perhaps during musth, males are signalling that they place a very high value on oestrous females, whereas non-musth males, no matter how old or large, are signalling that they place a lower value on receptive females. In this paper, the three different signalling functions of musth, fighting ability, intentions or intentions as a corollary of resource value, will be evaluated. Parker & Rubenstein's model is used to predict temporal patterns of musth among males of different rank.

Background: Patterns of Musth in Amboseli

Male African elephants over approximately 25 years of age (ageing techniques are described below and in Poole 1987) exhibit extended periods of sexual activity and inactivity defined in terms of hormonal changes and association patterns (Poole et al. 1984; Hall-Martin 1987; Poole 1987). During sexually active periods, male elephants move from group to group in search of oestrous females (Barnes 1982; Hall-Martin 1987; Poole & Moss, in press). Among older males, some proportion of the sexually active period is spent in the heightened sexual and aggressive state of musth. The dramatic increase in aggression exhibited by musth males (Asian elephants, *Elephas maximus*: Jainudeen et al. 1972a, b; African elephants: Hall-Martin 1987;

Poole 1987) is associated with, and perhaps caused by, extremely high levels of circulating testosterone which may be 50-fold the non-musth levels (Asian elephants: Jainudeen et al. 1972b; African elephants: Hall-Martin & van der Walt 1984; Poole et al. 1984).

The occurrence and duration of musth is related to age: in the Amboseli population no male under 24 years old has been seen in musth; bouts of musth among individuals 25–35 years old are short and sporadic (several days to weeks), while older males experience longer (2–5 months), more predictable periods of musth on an annual basis (Poole 1987). Musth males can be observed year-round, although the frequency of musth is highest during and following the rainy seasons. The number of males in musth per month correlates closely with the number of females observed in oestrus (Poole 1987). Since the period of oestrus lasts only 4–6 days (Moss 1983) and musth may last several months, the onset of musth in a male is not necessarily triggered by the onset of oestrus in a particular female (Poole 1987). Exceptions occur among smaller males who may be observed to come into musth (onset of signalling) within a few hours of finding an unguarded oestrous female (Poole, unpublished data).

The musth periods of different males are asynchronous and each male comes into musth at a specific time every year. The timing of a male's musth period is relatively consistent from one year to the next, particularly among older individuals. However, gradual changes do occur as an individual rises or falls in rank and moves into a reproductively better or worse time of the year (Poole 1987). Similar patterns hold for Asian elephants (see Eisenberg et al. 1971; Eisenberg & Lockhart 1972; Jainudeen et al. 1972a, b; Gale 1974; Kurt 1974; reviewed by Poole 1987).

During mid oestrus females go into consort with a musth male who guards her from the attempts of lower-ranking males to obtain copulations (Poole, in press). Males in musth are more successful at obtaining matings for two reasons: females prefer musth males (Moss 1983; Poole, in press) and males in musth rank above non-musth males in agonistic interactions (see below).

METHODS

Study Area and the Amboseli Population

Observations were made on a population of free-

ranging African elephants from January 1976 to June 1986 in Amboseli National Park, Kenya. An intensive study of musth was carried out from January 1980 to July 1981 and from December 1984 to June 1986. The Amboseli ecosystem consists of semi-arid wooded, bushed and open grasslands interspersed with a series of permanent swamps. Rain falls in two distinct seasons and averages 350 mm a year.

Amboseli National Park and the surrounding area is inhabited by a population of elephants presently numbering 670 individuals, including 52 matriarchal families and 160 independent adult males. All elephants are known individually.

Male elephants continue to grow until late in life, and age can be estimated by shoulder height, tooth eruption (Laws 1966) or from hind footprint length (Western et al. 1983; Lee & Moss 1986). The ageing techniques used in this study are described in Poole (1987). The accuracy of ages attributed to males is ±3 years. Males were divided into five age classes: class 1A: 10–14·9 years ($N=23$); class 1B: 15–19·9 ($N=47$); class 2: 20–24·9 ($N=42$); class 3: 25–34·9 ($N=36$); class 4: 35–49·9 ($N=19$); class 5: 50+ ($N=2$). The numbers of individuals in each class are from June 1986 records. By 25 years of age, males have grown to approximately 80% of their asymptotic height of 330 cm (Laws 1966; Poole, unpublished data), but to only 55% of their asymptotic weight of 6000 kg (Laws 1966).

Sampling Methods and Analyses

Focal sampling

During the 1980–1981 study period, 754 half-hour focal samples (Altmann 1974) were made of the 30 largest adult males; 323 of these samples were of males in musth. During the 1985–1986 study period an additional 200 3-h focal samples were completed on musth males.

Monitoring urine and weight loss

To monitor the changing sexual state of the large adult males, I recorded detailed information on the presence or absence of temporal gland secretion (on a scale of 0–4), temporal gland swelling (on a scale of 0–3), and urine dribbling (on a scale of 0–10). The rate of urine loss was estimated by on-the-minute point sampling during focal samples (see Poole 1987 for descriptions of the different scores). The volume of urine per min was estimated by stimulating each score with water from a tap. Estimates for each score are means based on 10

trials and range from $0=0$ to $10=5·7\pm0·4$ litres/min.

To obtain estimates of condition loss during musth, I photographed each male at musth onset and termination and, on the photograph, I measured the ratio of the elephant's body width to height. In addition, each focal male's condition was estimated visually on a scale of 1–6 on every day that the male was sighted as follows.

(1) Emaciated: no male was ever assigned a score of 1.

(2) Very thin: the shoulder blades, pelvic bone and backbone protrude.

(3) Thin: the shoulder blades, pelvic bone and backbone are noticeable.

(4) Good: slight sinking in front of the pelvic bone is noticeable and the backbone and shoulder blades protrude slightly.

(5) Fat: there is no sign of shoulder blades, pelvic bone or backbone.

(6) Very fat: there is no sign of shoulder blades, pelvic bone or backbone and fat hangs from the male's belly.

Association index

The strength of association between pairs of sexually active males was taken as the total number of days that a pair of males was seen together (T) in a group of females, divided by the number of days (D) male I ($D(I)$) was seen in female groups, plus the number of days male J ($D(J)$) was seen in female groups, minus the number of days they were seen together with females ($T/D(J)+D(J)-T$). This method allows for the possibility of double counting, thus increasing the denominator and decreasing the strength of association (Ginsberg & Young, unpublished data). However, only a small proportion of the referenced males were in fact seen in different female groups on the same day.

Determining non-musth agonistic dominance rank

Interactions observed between a pair of males on a particular day were not scored as independent, therefore dyadic dominance was determined by the male who won on a greater number of the days that the pair was seen interacting. These were referred to as interaction-days. Based on the outcome of interactions between pairs of non-musth males, I assigned relative ranks to individuals from a matrix in which the highest number of points fell on one side of the line. For those dyads in which non-musth reversals were observed, the male who won

the higher proportion of total interactions was considered the higher ranking of the two. I include only interactions that began with one of the behaviours defined as threats. Threats include ear-folding, ear-waving, shaking the head or holding it up high, tossing the trunk, walking towards another elephant with the head high and ears extended, folded or waving, and chasing or tusk-ing. The receiving individual would either look away or walk away, with head and ears low.

Retreat distance

During dyadic agonistic interactions I recorded the distance at which the subordinate elephant began to retreat from a male who was threatening him by walking toward him. Only bouts of one interaction were included in this analysis. I selected the first interaction recorded between any two individuals during the 1980–1981 study period, so that each pair of males was counted only once.

RESULTS

Agonistic Dominance and Musth

Musth males exhibited higher rates of aggression than did other sexually active, but non-musth, males (Mann–Whitney U-test, $U = 43·0$, $N_1 = 9$, $N_2 = 16$, $P < 0·05$). The median frequency of ago-nistic interactions per h by musth males was 7·5 (interquartile range = 6·4–8·4), while the median frequency for non-musth males was 3·5 (interquar-tile range = 0·9–7·3).

The factor determining dominance rank between non-musth males was body size (Spearman rank correlation $r_s = 0·99$, $N = 37$, $P < 0·01$; Fig. 1), with larger males ranking above smaller males in dyadic interactions (number of interaction-days = 574). When both of a pair of males were in musth, the winner of an interaction was also usually deter-mined by body size. During interactions between 75 different pairs of musth males the interactions were won by the larger male in 70 (93%) pairs ($\chi^2 = 56·4$, $df = 1$, $P < 0·001$; number of interaction-days = 129).

However, during aggressive interactions between males where one of a pair was in musth and the other was not, the winner was determined by musth, rather than by body size. For example, examining only the cases where the smaller male was in musth and the larger male was not in musth, in 42 (86%) different pairs the smaller musth male won, while the larger non-musth male won in only
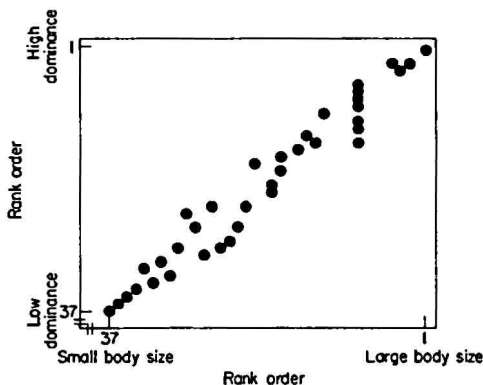

Figure 1. Relationship between body size rank and agonistic dominance rank among non-musth males. There is a significant correlation between the two vari-ables with larger males ranking above smaller males in dyadic interactions.

seven different pairs ($\chi^2 = 25$, $df = 1$, $P < 0·001$; number of different pairs = 49; number of interac-tion-days = 53). During 1984–1986, I recorded the condition of focal males; thus I was able to compare the difference in body condition for 20 interacting pairs. The smaller, winning musth male had been assigned a better condition score than the larger non-musth male in only three (15%) cases. In six cases they were scored the same, while in 11 (55%) instances the smaller, winning musth male had actually been in visibly poorer condition (sign test, $x = 3$, $N = 14$, $P = 0·03$).

The retreat distances of non-musth males (classes 4, 3 and 2) from a standard threat (walking toward another male with the head high and ears extended) given by class-4 musth and non-musth males, suggest that males not only believe the musth announcement of aggression, but that they are able to assess the probability of escalation. Both class-3 and class-4 males retreated at greater distances from class-4 musth males than they did from class-4 non-musth males (class 4: Mann–Whitney U-test, $U = 8·0$, $N_1 = 16$, $N_2 = 20$, $P < 0·001$; class 3: $U = 1$, $N_1 = 48$, $N_2 = 6$, $P < 0·001$; Fig. 2), while among class-2 males, where there was little risk of attack by the very much larger class-4 males, there was no difference in the distances that they retreated from musth or non-musth class-4 males ($U = 37·5$, $N_1 = 36$, $N_2 = 3$, NS; Fig. 2).

Frequency of Musth: Suppression and Avoidance

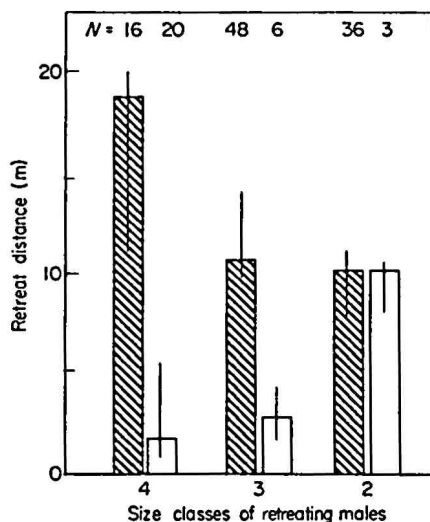Ninety-nine of the adult males ($N = 170$) were

Figure 2. Histograms of retreat distances by males from classes 4, 3 and 2, from a standard threat (walking towards another elephant with the head high and ears extended) given by musth and non-musth class-4 males. Males from both classes 3 and 4 retreated at greater distances from class-4 musth males than they did from class-4 non-musth males, while among class-2 males, where there was little risk of attack by the much larger class-4 males, there was no difference in the distances that they retreated from musth or non-musth class-4 males. Open bars: in all-male groups from a class 4 non-musth male; hatched bars: in female groups from a class 4-musth male. Median distances and interquartile ranges are given.

Figure 3. Frequency distribution of the number of different males observed in musth per month over a period of 10 years.

over 20 years old and competed actively for access to oestrous females. Only 37 of these males came into musth periodically. Since the musth periods of males were not synchronous, typically only a few males were in musth simultaneously. A mean (and mode) of three males were observed in musth per month. Figure 3 shows the frequency distribution of musth males per month.

There is behavioural evidence that the sporadic nature of musth among lower-ranking individuals is due to suppression by higher-ranking males. On many occasions I watched large musth males repeatedly threaten or chase (often for several kilometres) lower-ranking individuals, who were also in musth, until the subordinate male either stopped signalling (urine dribbling ceased immediately, temporal gland secretion dried up and the male adopted a head-low, non-musth posture) or left the group and went elsewhere. The results of harassment of smaller males by larger males can be
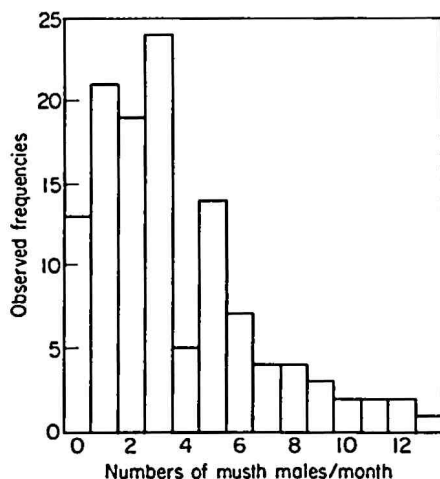
seen by examining the musth and association patterns of some of the smaller males (Fig. 4). Smaller males were seen in musth significantly more often when a higher-ranking musth male was absent than when one was present (Wilcoxon matched-pairs signed-ranks test, $T=0$, $N=6$, $P<0.05$). Similarly, they were seen out of musth significantly more often when there was a higher-ranking musth male present than when one was absent ($T=0$, $N=6$, $P<0.05$).

Rather than dropping out of musth when challenged, large males in musth appeared to try to avoid the company of other large musth males. Males accomplished this either by coming into musth at different times of the year (see Poole 1987) or, if their musth periods overlapped, by using different areas. Table I shows the total number of days that the musth periods of different large males overlapped (in 1980–1981) and the number of days that each male was seen with another.

That large musth males attempted to avoid other large musth males can also be seen by comparing the association indices between seven large males and other large males (during musth), with the same large musth males and smaller non-musth males. Each of the seven large musth males had a higher median association index with smaller non-musth males than they did with other large musth males (Wilcoxon test, $T=0$, $N=7$, $P<0.05$; Table II).
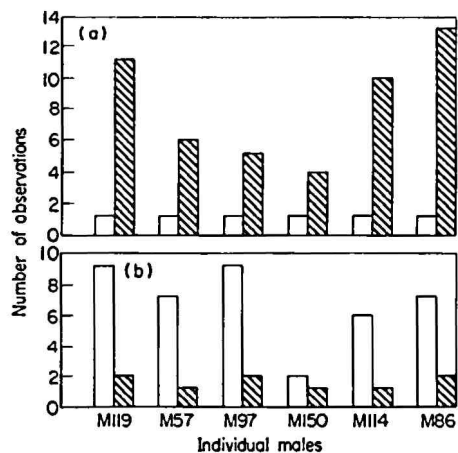
Figure 4. Frequency histograms of observations of (a) musth or (b) non-musth among the smaller class-4 males depending upon whether a larger musth male was present (open bars) or absent (hatched bars) (1980–1981). Smaller males were seen in musth significantly more often when a higher-ranking musth male was absent than when one was present. Similarly, the same males were seen out of musth significantly more often when there was a higher-ranking musth male present than when one was absent.

Chases and Escalated Contests

In 440 h of focal sampling on musth males in groups (during 1985 and 1986), 1039 agonistic interactions involving at least one musth male were observed (excluding escalated contests). Musth males were more aggressive towards other musth males than they were toward non-musth males. Chases were observed in a higher proportion of interactions involving two musth males (26 chases; $N=216$) than during interactions between a musth and a non-musth male (33 chases; $N=823$; $\chi^2=19 \cdot 1$, $df=1$, $P<0 \cdot 001$).

Although males in musth are aggressive, escalated contests are extremely rare. In 14 years of observations, only 31 escalated contests have been witnessed. Of these, 20 were between pairs of musth males, three were between pairs of sexually active, non-musth males and eight were between a musth and a sexually active non-musth male. Sexually inactive males were never observed in escalated contests. In the fights between a musth and non-musth male, the musth male was the smaller of the pair in seven of the eight fights, and six of these were won by the smaller musth male. Although these data suggest that being in musth is associated with an increase in the ability actually to win fights,

three of the six fights involved one young male who, on his first recorded day in musth, attacked four larger males in a 2-h period; he won three fights in succession and lost the last.

Fights between two musth males usually occurred between similar-sized individuals (Fig. 5). Of the 20 fights observed between musth males, the outcome was conclusive in 15. In 10 of these fights, there was a difference of less than 6 cm in shoulder height between the two males and, in seven of these, the male who had been in musth for the shorter length of time won.

Two of the 20 fights observed between males in musth resulted in the death of one contestant. In a third fight a male was blinded in one eye, and, in several, males incurred tusk breakage and puncture wounds. There also appeared to be a thermoregulatory cost associated with fighting. As body size increases the ratio of the surface area to volume decreases, and therefore the rate of metabolic heat loss declines (Calow 1977). All of the fights that I witnessed occurred in the middle of the day in areas with no shade. One fight lasted 6 h, another for 4 h and several lasted over 1 h. When males were not locked in combat, they bashed bushes, tossed logs, tusked the ground and walked in parallel. Many individuals were visibly heat stressed and went to the nearest mud-wallow or water-hole as soon as the fight was over. All fights ended with the victor chasing the loser several kilometres. As a result the loser usually did not have access to water until after the winner.

Economics of Musth

To examine weight loss during musth, I used a visual estimate of body condition and compared the score assigned on the date of musth onset with that given at the end of a male's musth period. All but two males (these two males were in musth for only 10 and 18 days) showed a decline in condition (sign test, $x=2$, $N=22$, $P<0 \cdot 001$). It also appeared that weight loss increased as the duration of musth lengthened (Spearman rank correlation $r_s=0 \cdot 74$, $N=23$, $P<0 \cdot 01$; Fig. 6). In addition, the two males who declined three points on the condition index did not come into musth the following year. Males in poor condition who were involved in fights usually dropped out of musth several days after fighting (Fig. 6).

During musth, males spent significantly less time feeding (Wilcoxon matched-pairs signed-ranks

Table I. The number of days that the musth periods of each pair of males overlapped and, in parentheses, the number of days that each pair was observed together (1980–1981)

Males	|13	28	126	22	41	117	73	44	99	45
13	—	70	30	30	66(1)	50(1)	0	38	148(7)	23(1)
28		—	113	6	35	67	31(1)	53	52	2
126			—	0	17	34	0	76	11	18
22				—	44	0	0	0	1	0
41					—	28	0	25(1)	30	23(1)
117						—	0	28	37	23
73							—	0	0	0
44								—	18(1)	23
99									—	13
45										—
Days*	61	22	17	21	23	13	11	5	28	7

* The number of days each male was seen in musth by the observer in 1980–1981.

Table II. Association index matrices between sexually active males; the median association indices for large musth males with other large musth males (a) is compared with the median indices of the same large musth males with smaller sexually active non-musth males (b)

| Males	Large musth males						
	13	28	22	41	117	73	99
(a) Large musth males							
13	—						
28	0·03	—					
22	0·03	0	—				
41	0·02	0	0	—			
117	0·02	0	0	0	—		
73	0	0·04	0	0	0	—	
99	0·11	0	0·08	0·03	0	0	—
126	0	0	0	0	0	0	0
Median	0·02	0	0	0	0	0	0
(b) Smaller non-musth males							
173	0·15	0·03	0·06	0	0·04	0	0·14
91	0·16	0·02	0·02	0	0·07	0·04	0·14
174	0·06	0	0	0	0	0·14	0
49	0·19	0	0·15	0	0·02	0	0·15
79	0	0·14	0·07	0	0	0·14	0·02
157	0·07	0·04	0·07	0·04	0·08	0	0·03
149	0·22	0·02	0·07	0·05	0·05	0·02	0·12
132	0·19	0·01	0·06	0·03	0·05	0·04	0·14
Median	0·15	0·02	0·07	0	0·05	0·03	0·13
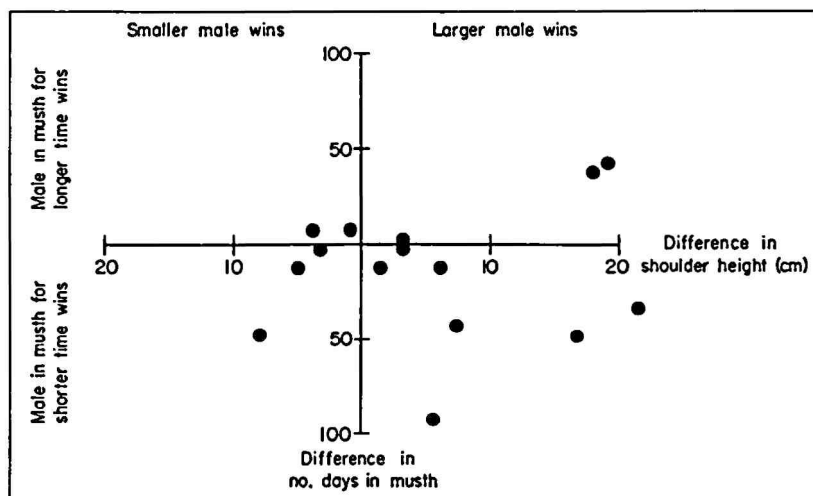
Figure 5. Asymmetries in body size and condition are presented in relation to fighting ability in 15 escalated contests between musth males. The X-axis represents differences in shoulder height (cm) while the Y-axis represents differences in body condition. Since condition scores were not assigned in the early part of the study, a male in better condition was taken as the male who had been in musth for the shorter length of time. Thus, relative condition is given as the difference in the number of days the opponents had been in musth.
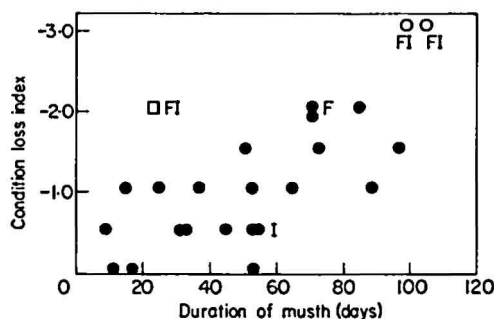
Figure 6. Relationship between the duration of a male's musth period and the degree of condition loss during the 1985–1986 study period. □: died as a result of injury received in a fight; ○: did not come into musth the following year; F: dropped out of musth within a few days of fighting; I: injured in a fight. There is a significant correlation between the two variables. The male who died was not included in this analysis since his rapid weight loss was apparently due largely to his inability to feed after his trunk was punctured in a fight.
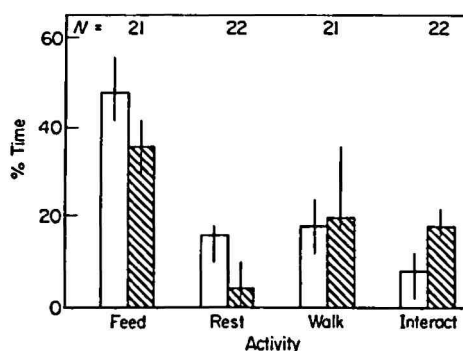

Figure 7. Histograms showing the percentage of time spent feeding, resting, walking and interacting by males during musth (hatched) and non-musth (open) periods. During musth, males spent significantly less time feeding and resting and more time walking and interacting with other elephants than when not in musth. Medians and interquartile ranges are given.

test, $T=21$, $N=22$, $P<0.01$) and resting ($T=12$, $N=22$, $P<0.01$) and more time walking ($T=44$, $N=21$, $P<0.02$) and interacting with other elephants ($T=5$, $N=22$, $P<0.01$) than when not in musth (Fig. 7). Although weight loss during musth may be largely attributed to the increased activity

levels and decreased feeding, captive Asian elephants lose weight during musth even when they are chained and given normal rations of food (Deraniyagala 1955). Since musth is associated with elevated levels of circulating testosterone, weight loss may also be related to the increase in metobolic rate that is associated with high androgen levels (Bell et al. 1976).

Like many other rutting mammals (reviewed by Coblentz 1976; Gosling 1985), male elephants mark themselves and the area they use with a strong-smelling urinary discharge. However, unlike territorial species where males mark only specific points of the defended area with glandular secretions, dung or urine (e.g. Gosling 1985), elephants leave a trail of urine marking the path that they have taken. Obviously, if the purpose of scent marking is to leave a trail for other individuals (both males and females inspect urine trails of musth males) it will function optimally if the trail is continuous. However, since urine is, probably, limited, particularly in arid environments where water may be in short supply and/or distant, individuals might be expected to conserve urine by altering the rate of discharge depending on the distance travelled. To test this hypothesis, I looked at the difference in dribbling rates when males were moving slowly while feeding versus when walking. Each male examined ($N = 14$) showed a higher rate of urine loss when walking (median rate = 6, interquartile range = 5–6) than while feeding (median rate = 3, interquartile range = 2–4; Wilcoxon matched-pairs signed-ranks test, $T = 0$, $N = 14$, $P < 0.01$). Each male contributed at least five 3-h samples.

If body size poses a physiological constraint to the volume of urine a male can leave in a trail, then we would expect large males, with a bigger reservoir, to lose urine at a higher rate than smaller males. Large males 40 (± 3) years and older left a larger volume of urine per unit time (median = 0.24 litres/min, interquartile range = 0.21–0.26) than did smaller males of less than 40 (± 3) years (median = 0.10 litres/min, interquartile range = 0.09–0.20; Mann–Whitney U-test, $U = 8$, $N_1 = 8$, $N_2 = 11$, $P = 0.002$), suggesting that smaller males may not signal at a higher level because they are physiologically unable to do so.

Since the loss of urine associated with signalling during musth (median for large males = 345 litres per 24 h; median for small males = 144 litres per 24 h) is greater than the loss during normal urination by non-musth males (approximately 5 litres 14 times per day = 70 litres: Benedict 1936; Poole, unpublished data) the frequency of drinking during musth and non-musth periods was examined. During musth, males drank more frequently than during non-musth (Wilcoxon matched-pairs signed-ranks test, $T = 10$, $N = 12$, $P = 0.02$). The median percentage of focal samples in which musth

males drank was 26% (interquartile range = 12–46), while the median percentage during non-musth was 10% (interquartile range = 0–16) suggesting a cost associated with urine-marking.

Musth as a Signal of Resource Value

Parker & Rubenstein's model (1981) of animal conflicts where an interaction exists between fighting ability and resource value can be applied to the Amboseli data to see whether the predictions satisfactorily explain the observed patterns of musth and the behaviour of male elephants. In this model opponents sustain costs (K) at rates K_A and K_B and their values of winning (V) are V_A and V_B. An evolutionarily stable strategy exists of the rule 'fight on estimating role A, where $V_A/K_A > V_B/K_B$; retreat if B'.

In the Amboseli population the mean numbers of conceptions (based on births 21.5 months later) were 30 during the 6 months from February through July and 15 from August through January ($N = 9$ years; Amboseli Elephant Project, unpublished data). For the purposes of this discussion I will refer to February through July as the wet season and August through January as the dry season. In this model it is assumed that all males have an equal chance of finding a particular oestrous female. A high-ranking male guards and mates any receptive female he locates; a medium-ranking male obtains any female he finds that is not already guarded by a high-ranking male; a low-ranking male gets any female he finds that is not already guarded by a medium- or high-ranking male. If all males have a 75% chance of finding a particular female, then the reward gained (V) in terms of number of oestrous females monopolized can be expressed as in Table III.

Musth is associated with two costs (K) which reduce future fitness. During musth, all males suffer considerable loss of condition and escalated contests may result in a decline in rank, or in injury or death. If we assume, initially, that all males stay in musth for the same length of time, then the cost associated with loss of condition and urine dribbling will be the same for all males. In the dry season, however, males will have to go further for water, therefore I have assumed that the physiological cost is higher in the dry season than in the wet season. I have assumed further that the reduction in fitness due to escalated contests is higher for low-ranking males, since they are more likely to meet

Table III. The relative rewards gained (V) in terms of the number of oestrous females monopolized in the wet and dry season for high-, medium-and low-ranking males

	Male rank		
	High	Medium	Low
Probability of locating a particular female	0·75	0·75	0·75
Proportion of oestrous females monopolized	0·75	0·19	0·06
No. of oestrous females monopolized			
Wet season	22	6	2
Dry season	11	3	1

Table IV. The relative costs (K) for males of different ranks during the wet and dry seasons

Costs	Wet season: Male rank			Dry season: Male rank		
	High	Medium	Low	High	Medium	Low
Condition loss	10	10	10	15	15	15
Fighting	5	10	15	5	10	15
Total	15	20	25	20	25	30

Table V. The 2-year payoffs (V/K) for high-, medium- and low-ranking males

Occurrence of musth	Male rank		
	High	Medium	Low
Full year in alternate years	0·9	0·2	0·05
Wet season in both years	1·5	0·3	0·08
Dry season in both years	0·6	0·1	0·03

males of equal or higher rank than are high-ranking males. In addition, since reproductive success increases dramatically late in life (Poole, in press), small males have relatively more to lose in terms of reduced future fitness if they are injured or die in a fight. The relative costs of musth for males of different ranks during different seasons can be scaled as in Table IV.

Assuming that physiological costs prevent males from being in musth continuously, three possible strategies are examined: (1) stay in musth for a full year, but come into musth only during alternate years; (2) come into musth each year but only during the wet season; (3) come into musth each year but only in the dry season. The 2-year payoffs for high- (V_h/K_h), medium- (V_m/K_m) and low- (V_l/K_l) ranking males in each strategy are as in Table V.

Thus, the relative payoffs for males of each rank are greatest when they come into musth only during the wet seasons. Clearly, high-ranking males do best by coming into musth only in the wet season, and, given that this is the strategy they use, how does their action affect the relative payoffs for medium-ranking males? Note that since now there are no high-ranking males in musth during the dry season, medium-ranking males assume the resource values and costs of high-ranking males during that season: full year in alternate years, $V_m/K_m = 0·4$; wet season in both years, $V_m/K_m = 0·3$; dry season in both years, $V_m/K_m = 0·6$.

Therefore, if high-ranking males come into musth only during the wet season, the relative payoff for medium-ranking males becomes highest in the dry season. Given that high-ranking males come into musth only during the wet season and medium-ranking males come into musth only during the dry season, the best payoff for low-ranking males arises only if they come into musth during the wet season, overlapping with the high-ranking males: full year in alternate years, $V_l/K_l = 0·2$; wet season both years, $V_l/K_l = 0·3$; dry season both years, $V_l/K_l = 0·1$.

But, since low-ranking males are competing with the highest-ranking males and faring relatively badly, could they do better by retracting the musth announcement when in association with higher-ranking males or when challenged? If the cost of musth is decreased by half (lowered physiological cost due to the shorter duration of musth and a decrease in the costs resulting from fighting, since low-ranking males retract the musth announcement and thus avoid challenges by higher-ranking males) then the relative payoff for low-ranking males in the wet season would become 0·6. Thus, low-ranking males can increase their relative payoff by retracting their announcement of aggression.

DISCUSSION

Predictions derived from game theory suggest that during conflict situations animals should not signal their intention to attack since such signals can be

exaggerated without cost (except in so far as escalation leads to injury) and would, therefore, be open to evolutionary cheating. However, signals do exist which apparently announce aggressive intent and the phenomenon of musth provides a useful system to look at the possibility of honest signalling. Three possible signal functions of musth, fighting ability, intentions and intentions as a corollary of resource value, are examined in turn.

Relative fighting ability is not a satisfactory explanation of musth since, in Amboseli, small musth males were able to dominate larger, normally higher-ranking, non-musth males. Large non-musth males who were apparently in peak condition often fled for several kilometres from much smaller, musth males who were in visibly poorer condition. The asymmetries in body size and condition were often so great that it is hard to believe that the decision to flee was based on relative fighting ability.

The behaviour of male elephants suggests that musth males are indeed signalling aggressive intent. However, the ability of younger, smaller musth males to retract their announcement of aggression when challenged by a much larger musth male, raises the question of cheating (Maynard Smith 1982). However, males who stopped signalling while in the presence of a higher-ranking musth male still exhibited the very high musth concentrations of urinary testosterone (Poole et al. 1984). Comparable behaviour has been observed among Pere David's deer (Wemmer et al. 1983) and red deer (Walther 1984) where one of the ways that rutting males signal aggression is by dilation of the preorbital gland. Males are able to dilate the gland at will and subordinate males close their gland when in the presence of a higher-ranking male.

van Rhijn (1980) and van Rhijn & Vodegel (1980) have argued that if individual recognition and past experiences play a role in assessment, then bluff is unlikely to evolve since exaggerating individuals will be recognized as doing so. Elephants are long-lived, intelligent and highly social animals and individual males meet and interact with all other members of a small population frequently (Moss & Poole 1983). Recent studies have shown that elephants are able to recognize other individuals vocally and olfactorally (Poole, unpublished data), making it unlikely that elephants could cheat. However, the rapidly changing ranks of males, and the different retreat distances shown by males, suggest that individuals are accurately assessing the likelihood of aggressive behaviour. Perhaps the solution to why signalling aggressive intent remains effective and non-bluffable might be better understood by accounting for the lifetime reproductive potential and the fluctuating resource value of male elephants.

Parker & Rubenstein (1981) examined the case in animal conflicts where an interaction exists between flighting ability and resource value. They suggested that if individuals could estimate correctly their relative roles then escalation could be avoided. However, they felt it would be difficult for individuals to assess resource value accurately, particularly if it were correlated with some physiological condition rather than with ownership. Musth may be an example where resource value is correlated with a physiological condition, and announced by means of a reliable signal which allows individuals to assess whether they are in role A or role B, where the rule is 'fight on estimating role A, where $V_A/K_A > V_B/K_B$; retreat if B'. The low rate of escalated contests (31 in 14 years of observations) suggests that the signals associated with musth allow individuals to make relatively accurate estimates of their respective roles. The ability of small musth males to dominate larger non-musth males may occur when the time-specific value placed on winning by the smaller male is great enough, and the value placed on winning by the larger males is small enough, to override the difference in fighting ability.

In the simple model that I presented in this paper I did not take into account the numbers of males in each rank, nor an accurate distribution of oestrous females in time and space; however, the model predicts the observed temporal patterns of musth (Poole 1987) and the behaviour of male elephants relatively accurately. In Amboseli, the highest-ranking males all came into musth during the wet season. While some medium-ranking males also came into musth during the wet season, those that came into musth during the dry season stayed in musth for longer with the result that they guarded as many oestrous females as medium-ranking males who had their musth periods in the wet season (Poole, unpublished data). The majority of low-ranking males came into musth during the wet season, but their bouts of musth were short and sporadic (Poole 1987).

Reproductive success of male elephants increases rapidly late in life due to continued male growth and the relationship between body size and

dominance. Thus males who live to an old age have a significantly higher lifetime reproductive success than do males who die when they are still relatively young (Poole, in press). Since fights frequently lead to injury or death (see also Hall-Martin 1987), thereby reducing future reproductive potential, elephants should clearly signal, by not being in musth, that they will not fight when the benefits derived from winning are relatively less than they could achieve either at a different time of year or at a later stage in life. Since the number and fighting ability of males in musth changes frequently, males must continually reassess their role in each asymmetry. It is likely that males are able to avoid other musth males by whom they would be attacked by inspecting their urine trails (Poole, unpublished data) and by listening for their low-frequency calls (Poole 1987).

Elephants provide an unusual opportunity to examine aggressive signalling and resource value because their reproductive effort is spread over many years and, unlike rutting ungulates in the temperate zone, the sexually active periods of male elephants are asynchronous. However, opportunities for studying honest signalling probably exist in a wide variety of ungulates, particularly in the tropics where asynchrony in breeding condition is more likely to manifest itself in females and therefore also among males (e.g. *Axix axis*: Eisenberg & Lockhart 1972; *Cervus unicolor*: Whitehead 1972; *Taurotragus oryx*: Hillman 1976).

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