

Mate guarding, reproductive success and female choice in African elephants

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Abstract. Male guarding of females, male mating success and female choice were studied for 8 years among a population of African elephants, *Loxodonta africana*. Males were not able to compete successfully for access to oestrous females until approximately 25 years of age. Males between 25 and 35 years of age obtained matings during early and late oestrus, but rarely in mid-oestrus. Large musth males over 35 years old guarded females in mid-oestrus. Larger, older males ranked above younger, smaller males and the number of females guarded by males increased rapidly late in life. Body size and longevity are considered important factors in determining the lifetime reproductive success of male elephants. Oestrous females exercised choice by soliciting guarding behaviour from musth, but not non-musth males. Females in mid-oestrus gave loud, very low frequency calls that may attract distant males and incite male-male competition. The behaviour of oestrous females resulted in their mating with males who were old, vigorous and healthy.

In species where there is strong competition between males for access to females, and where large body size confers advantages in contests between males, sexual dimorphism is pronounced (Darwin 1871). Large males in these species frequently enjoy a higher mating success than do smaller males (e.g. Le Beouf 1974; Davies & Halliday 1979; Clutton-Brock et al. 1982). Sexual differences in body size are greater in large species (Clutton-Brock et al. 1977) and in the largest of land mammals, the African elephant, *Loxodonta africana*, males reach twice the weight of females (Laws 1966; Hanks 1972; Laws et al. 1975). Elephant mothers invest more heavily in male calves than they do in female calves, and early rapid growth combined with a higher rate of growth in males throughout life, results in the large degree of sexual dimorphism (Lee & Moss 1986). In the first year of life male elephants suffer higher mortality than do females (Lee & Moss 1986) and higher mortality rates among males continue through much of life (Poole, unpublished data).

Male elephants continue to grow until late in life (Laws 1966). Although males are physiologically able to reproduce by 14-17 years of age (Laws 1969), these young males weigh less than half the weight of a 50-year-old male (Laws 1966) and are unable to compete successfully with older males for

access to receptive females (Poole 1982). Agonistic dominance correlates closely with body size, thus older males typically rank above younger males in agonistic encounters (Poole 1989). Since it takes many years for a male to become bigger than most other competitors, continued growth and longevity appear to be crucial factors in determining the lifetime reproductive success of male elephants.

Numerous studies have shown that female choice is also a powerful evolutionary force in many polygynous species (e.g. Andersson 1982; Kodric-Brown 1985; Hedrick 1986). In recent years, however, there has been much controversy over the way in which female mating preferences evolve (reviewed by Kirkpatrick 1987). The debate can generally be divided into two schools of thought: the good genes proponents argue that female mating preferences evolve to favour ecologically adapted males, while those who back the non-adaptive school postulate that preferences often cause male traits to evolve in ways that are non-adaptive with respect to their environment. The good genes school rests on the intuition that evolution should be adaptive and that the larger, more conspicuous and more vigorous males that are often favoured by sexual selection must, in some way, be better. In doing so they have often made assumptions about the heritability of the traits preferred by females. Despite this drawback, Hamilton & Zuk (1982) and Manning (1985) have

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suggested hypotheses which do lend support to the good genes school and are worth considering in the context of elephants.

In the Hamilton & Zuk (1982) model, disease affects the expression of the male trait thus allowing females to discriminate between males and choose the more vigorous males. The Manning (1985) model suggests that females who mate with young males mate with individuals carrying the average number of mutations, since natural selection has not yet had time to act on viability differences between males. Females who mate with older males, however, will tend to mate with individuals carrying fewer mutations, since only those males survive to an old age.

In this paper I have used data collected on known individuals over a period of 8 years to describe the mating patterns of African elephants and to examine the role of male-male competition and female preferences in shaping these patterns. The behaviour of female elephants appears to lend support to the hypotheses that suggest that females may select males on the basis of traits that indicate his condition and age.

METHODS

The social organization of African elephants has been described in detail elsewhere (Douglas-Hamilton 1972; Moss 1983; Moss & Poole 1983). Related female elephants live in stable groups known as family units (Buss 1961; Douglas-Hamilton 1972; Moss 1981). Above the level of the family are bond groups and clans (Moss & Poole 1983). Males gradually leave their natal family and, by approximately 14 years of age, begin to form the loose associations with non-natal families and other adult males that will characterize their adult life. During sexually active periods, adult males move widely in search of oestrous females, while during sexually inactive periods they are most often found in small groups with other adult males (Moss & Poole 1983; Hall-Martin 1987; Poole 1987). Among older males these alternating periods of sexual activity and inactivity are marked by the heightened sexual and aggressive state of musth (Poole & Moss 1981). During musth, males vocalize frequently, exhibit swollen and secreting temporal glands and leave a trail of strong-smelling urine (Poole 1987). The duration and intensity of a male's musth or rutting period is correlated closely with male age. Males in musth rank above larger,

normally higher ranking, non-musth males. Similarly, ranked musth males will fight if they meet one another (Poole 1989).

The social behaviour, population dynamics and ecology of a population of elephants in Amboseli National Park, Kenya, have been monitored since 1972. There are approximately 680 individually known elephants in the population, including 50 family units and 160 independent adult males. This paper is based on 8 years of data gathered from 1980 through 1987. All of the data were collected by me except a small proportion of the long-term records on mating and guarding. These data were collected by Cynthia Moss, Keith Lindsay, Phyllis Lee and Norah Njiraine who were all experienced elephant observers. Any inter-observer variability that existed would not affect the conclusions of the study. There was at least one person in the field during each month except October and November 1981, part of January-June 1982 and October 1986. I was engaged in a study of musth in Amboseli from January 1980 through July 1981 and from October 1984 through July 1987. The data collected in 1985 and 1986 are the most complete and I have used this subset for most analyses. Data on the rates of behaviour and on the distances between the oestrous female and the guarding male come from half-hour (1980-1981) and 3-h (1985-1986) focal samples (Altmann 1974) on musth and non-musth males.

Ageing Techniques

Male elephants continue to grow until late in life and age can be estimated by shoulder height and tooth eruption (Laws 1966) or from the length of the hind footprint (Western et al. 1983; Lee & Moss 1986). The ages attributed to males in this study were either known from birth records or have been estimated based on a combination of different methods: the degree of eruption and wear of teeth collected from elephants who died, the size and shape of the head in relation to body size, visual estimates of relative shoulder height, repeated measurements of footprint length over a period of 10 years and from photographs of known individuals taken in the early 1960s. The accuracy of ages attributed to males is ± 3 years. Males over 10 years old have been grouped in age classes which are as follows: 1a: 10-14.9 years; 1b: 15-19.9 years; 2: 20-24.5 years; 3: 25-34.9 years; 4: 35-49.9 years; 5: 50+ years.

Oestrus, Mating and Guarding

Short (1966) concluded that there were no external morphological signs of oestrus in the African elephant and that oestrus could only be detected when a female was seen mating. However, Poole (1982) and Moss (1983) found that oestrus could be identified by characteristic behaviour of both the female and accompanying males. Moss (1983) defined oestrus as the periodic manifestation of certain behaviours which included: wariness, the oestrous walk, the chase, mounting and consort behaviour. An oestrous period was defined as the occurrence of any of these behavioural categories on two or more days with a gap of no more than 14 days.

A successful mating was said to have occurred when evidence of intromission and ejaculation were observed. This was determined in four ways: (1) intromission was actually observed; (2) the male stayed mounted for 40–50 s with little movement by the female; (3) ejaculate exuded from the female's vagina; (4) a mount immediately followed by another chase indicated that the mount did not lead to a successful mating, while the male standing resting indicated a successful mating. At least two of these criteria had to be observed for a particular male to be scored as mating successfully. In addition, most, but not all, females gave a loud (102 dB recorded at 10 m and extrapolated to 5 m), very low frequency sequence of post-copulatory calls (Poole et al. 1988) after they had been mated.

Guarding was defined as behaviour on the part of a particular male which attempted to prevent rival males from obtaining access to an oestrous female. To be considered a guarder, a male must have been responsible for maintaining proximity to the female and must not have been observed avoiding any other male present. If a male satisfied the first, but not the second, criterion then he was considered a non-guarder. A female was described as attempting to solicit guarding behaviour from a particular male if she followed that male or if, when she was pursued by smaller males, she quickly moved to stand next to the larger male.

RESULTS

Male-Male Competition

Very few successful matings were observed among males in age classes 1 or 2 and the majority of matings were obtained by males in classes 4 and

Table I. The number of males and observed matings per age class*

	Age class					Total	
	1a	1b	2	3	4		5
Number of males	17	34	40	46	21	1	159
Number of matings	0	0	5	26	36	3	70

* The number of matings recorded in 1985–1986. The number of males in each age class is from June 1986. See text for definitions of age classes.

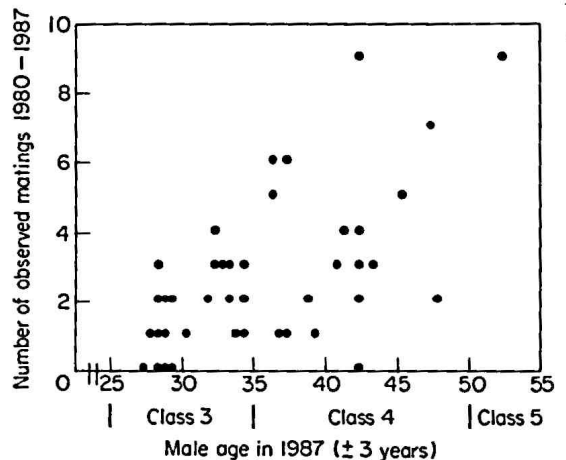


Figure 1. Relationship between male age and cumulative mating success from 1980 through 1987 among 41 males were at least 20 (± 3) years old in 1980. There is a significant positive relationship between the two variables (Spearman rank correlation $r_s=0.81$, $N=41$, $df=39$, $P<0.001$).

5. The 22 males (14% of adult males) in the two oldest age categories accounted for 54% of the successful matings during 1985 and 1986 (Table I). The cumulative number of matings observed from 1980 through 1987 by the 41 extant males who were over 20 ± 3 years old in 1980 is presented in Fig. 1. There is a significant positive relationship between male age and mating success (Spearman rank correlation $r_s=0.51$, $N=41$, $df=39$, $P<0.001$). The number of matings obtained by a male was not dependent on the number of days that he was seen in a group with an oestrous female (Spearman rank correlation $r_s=0.29$, $N=35$, $df=33$, $P=0.10$).

During 1985–1986 I observed 11 females on at least 4 days during their oestrous period and was able to monitor the pattern of male and female

Table II. The behaviour of females and associating males over the course of oestrus†

Oestrous females	Number of days observed					
	1	2	3	4	5	6
Zita	Mg	Mg	+Mgs; -Mg	-Nc*	—	—
Wairimu	*	Mg	Ms; -Mg	-Nc	—	—
Wayua	Mg	Mg*	Mg	-Nc*	Nc	—
Celeste	Mf	—	—	+Mg	Mg	-Nf
Lucia	Mg	Mg	Mg	—	-Nc*	—
Vida	Nc*	+Mg	Mg	Mgl; -Nf	—	—
Rebecca	Nf	+Mg	+Mg	Mg	-Nf	—
Audrey	Nc; +Mg	Mg	—	Mg	-Nf	—
Golda	Nf	+Mg	-Mg; +Mg	-Nf	—	—
Shirley	Mg*; +Mg*	Mg	-Mg	—	—	-Nf
Brenna	Mf	Mg	+Mg	Mg*	Mg	—

M: musth male; N: non-musth male; g: guards; c: chases; f: follows; *: mates; l: male leaves female; s: female solicits guarding; +: rank of male increases; -: rank of male decreases; no sign: no change in male; —: oestrous female not seen on that day.
 †: Note that day 1 indicates the first day that I saw a female in oestrus; it does not necessarily correspond to the female's first day of oestrus.

behaviour over the course of oestrus (Table II; note: day 1 is the first day that I observed the female in oestrus but does not necessarily imply her first day of oestrus). Early oestrus was associated with highly visible behaviour; the female was pursued by young males and protested against any attempt to mount her with a loud pulsated roar. On the 3 or 4 days in the middle of behavioural oestrus, females were guarded by males in musth. During this consort period the guarding musth male mated infrequently. In 129 h of focal sampling on musth males who were guarding oestrous females, I observed a total of 16 matings by guarders, at a rate of one mating per 8 h. Toward the end of behavioural oestrus the musth male left the female and she was then guarded and pursued by increasingly lower ranking males. During early and late oestrus large musth males showed little interest in the female.

During 1985–1986, 75 different females were observed on at least 1 day of oestrus (mean number of days observed was 2 ± 1 ; range 1–6). Seventy of these females were observed being guarded by a male on at least 1 day of their oestrous period. All except two of the guarding males were in musth. Forty-four females were observed guarded by a single musth male, while 24 females were guarded by more than one musth male.

During early and late oestrus, females were not guarded and were frequently chased and sometimes

mated with young non-musth males. During 1985–1986, I observed unguarded oestrous females on 52 days during which I observed 16 matings with non-musth males and no matings with musth males.

In mid-oestrus, females were guarded and mated primarily with the guarding males. I observed oestrous females being guarded on 127 days. On 119 (94%) days the guarders were in musth. Of the 49 matings that I observed when an oestrous female was being guarded by a musth male, 38 were by the guarding musth male while 11 were obtained by non-guarders. In one instance the guarding male lagged behind the female and a younger male was able to obtain a copulation. In five cases the guarder left the female's side to threaten or fight with another male, and in another five cases the guarder had moved off to test or pursue another oestrous female. On 8 days I observed oestrous females being guarded by non-musth males; these non-musth guarders were observed mating four times.

Males in classes 4 and 5 accounted for 89% of the observations of guarding behaviour ($N=127$). Since the behaviour of elephants suggests that the overall number of matings may be less important than who guards and mates with a female during mid-oestrus, I have examined the cumulative number of females guarded from 1980 through 1987 by the 41 extant males who were over 20 ± 3 years old in 1980. The ability to guard females

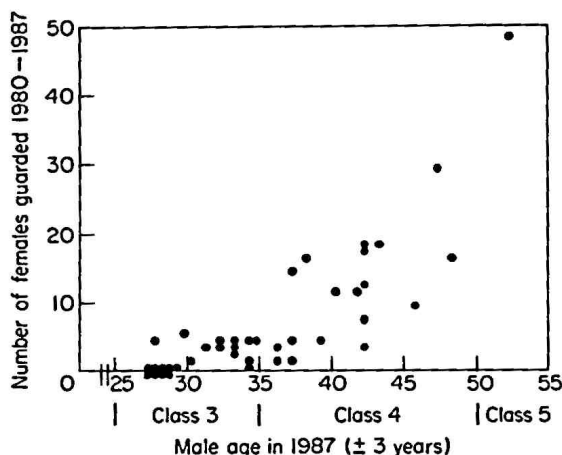


Figure 2. Relationship between male age and guarding success from 1980 through 1987 among 41 males who were at least 20 (± 3) years old in 1980. There is a significant positive relationship between the two variables (Spearman rank correlation $r_s=0.51$, $N=41$, $df=39$, $P<0.001$).

during mid-oestrus was strongly correlated with male age (Spearman rank correlation $r_s=0.81$, $N=41$, $df=39$, $P<0.001$; Fig. 2) and guarding success increased rapidly late in life. The number of females guarded was not dependent on the number of days that males were observed in groups with oestrous females (Spearman rank correlation $r_s=0.013$, $N=35$, $df=33$, $P>0.20$).

To guard a female successfully the male must be able to prevent rival males from obtaining access to her. During focal samples collected in 1985-1986 on males who were guarding an oestrous female, the mean number of all other adult males present was 9.4 ± 9.4 ($N=49$) and the mean number of class 3, 4 or 5 males was 2.7 ± 1.9 ($N=49$). To prevent these males from obtaining access to and mating with the oestrous female, the guarding male had to be both larger and more aggressive (see Poole 1989) than the other males and keep close to the oestrous female. When a male was actively guarding, the median distance between the guarding musth male and the oestrous female was 9.1 m (interquartile range 6.8-10.8 m; $N=29$). This distance was similar when proximity between a large musth male and an oestrous female was maintained solely by the female in late oestrous (median=10.8 m, interquartile range 7.5-15.3; Mann-Whitney $U=65$, $N_1=6$, $N_2=29$, $P=0.17$).

Although females may be observed in oestrus at any time of the year, 72% of observed oestrus and 66% of conceptions (based on births 21.5 months

later) occurred in the 6 months from February through July (Table III). Of the 12 oldest and highest-ranking males, nine had musth periods which occurred each year during this time (see Poole 1987, 1989).

Female Choice

Oestrous females solicited guarding behaviour from musth males but rarely from non-musth males. On the 34 days ($N=179$) that oestrous females were observed soliciting guarding behaviour, they solicited guarding from musth males on 33 (97%) days. A female was observed soliciting guarding behaviour from a non-musth male only once ($\chi^2=30.1$; $N=34$, $df=1$, $P<0.001$).

Oestrous females frequently called during and after mating. Calling by females did not appear to depend on whether they were mated by a musth male (31 called, four did not) or by a non-musth male (14 called, eight did not; $\chi^2=3.7$, $df=1$, $N=57$, $P>0.05$), nor whether the same females were mated by the guarding male (29 called, seven did not) or by a non-guarder (16 called, five did not; $\chi^2=0.003$, $df=1$, $N=57$, $P>0.05$). However, regardless of who they were mated by, the females were more likely to call during the period when they were being guarded by a musth male in mid-oestrus (38 called, six did not) than during the period when they were unguarded (seven called, six did not; $\chi^2=4.6$, $df=1$, $N=57$, $P<0.05$).

DISCUSSION

Among species that show sexual dimorphism in body size, larger males frequently have a higher rate of mating success than do smaller males (e.g. elephant seals, *Mirounga angustirostris*: Cox & Le Boeuf 1977; common toads, *Bufo bufo*: Davies & Halliday 1979; red deer, *Cervus elaphus*: Clutton-Brock et al. 1982). Since most mammals reach full adult size soon after reproductive maturity, mating success typically peaks in middle-age males and then declines late in life (e.g. horses: Rubenstein 1986; red deer: Clutton-Brock et al. 1979). However, a number of primate studies have shown that males past their physical prime consorted with oestrous females at higher rates than expected based on their dominance rank (reviewed by Smuts 1987). Male elephants continue to grow in height, and particularly in weight, throughout most of their adult life. Since mortality rates among males

Table III. The frequency of conceptions and observed oestrus per month*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Observed oestrus													
Frequency	34	35	61	52	35	53	56	25	23	12	11	16	413
Percentage	8	8	15	13	9	13	14	6	5	3	3	4	
Conceptions													
Frequency	32	36	41	39	34	61	39	33	19	10	14	13	317
Percentage	9	10	11	10	9	16	10	9	5	3	4	4	

* The records of observed oestrus are from 1976-1986 and of conceptions (based on births 21.5 months later) from 1976-1984.

are relatively high, males who live to be old have few competitors in their size class. Given that selection has favoured continued growth, male elephant lifetime reproductive success is strongly dependent on longevity. Among the Amboseli elephants, both mating and guarding success increased dramatically late in life. In Macropods, where continued growth also occurs, reproductive success among males also depends on survival and maintaining a high growth rate (Jarman & Southwell 1986).

Older musth males were more successful than younger non-musth males at guarding receptive females from the attempts of other males to obtain copulations because they were generally larger and more aggressive. Males retreated at a greater distance from threats by musth males than from threats by non-musth males (Poole 1989). However, the ability of large musth males to mate successfully was also dependent on the behaviour of oestrous females.

As in elephant seals (Cox & Le Beouf 1977), female African elephants give a loud pulsated roar when chased by younger non-musth males (Poole & Moss, unpublished data). This call has the immediate effect of attracting the attention of nearby higher ranking males who threaten the lower ranking male and prevent him from mating. In addition, females appear to advertize their receptive state during mid-oestrus with a series of loud very low frequency calls. The transmission characteristics of such sounds make it likely that the oestrous or post-copulatory calls can be heard by elephants at distances of several kilometers (Payne et al. 1986; Poole et al. 1988). Using a series of playback experiments, present research is testing

the possibility that females may call during mid-oestrus to attract distant high-ranking males.

Oestrous females attempted to solicit guarding behaviour from musth, but not non-musth males and played an active role in maintaining close proximity to preferred males. It could be argued that females solicited guarding behaviour from older musth males only to prevent the constant harassment of younger, smaller non-musth males. However, if this were so, we would expect females to solicit guarding from non-musth males during late oestrus when there were no older musth males nearby. That they did not suggests that females were making an active attempt to avoid copulation by the younger males. Females facilitated matings with large musth males by standing still, while they attempted to outrun younger non-musth males (Poole 1982; Moss 1983), providing additional evidence that female elephants were exercising choice.

There is considerable evidence that musth is a reliable indicator of good condition. Undernourished male Asiatic elephants do not come into musth and some mahouts traditionally practise underfeeding males as a method of preventing males from coming into musth (Gale 1974). Male African elephants in poor condition do not come into musth and males with wounds or infections drop out of musth (Poole 1989, unpublished data). Female elephants may be using musth as an indicator of good condition. However, whether these preferences translate into healthy and viable offspring as suggested by Hamilton & Zuk (1982) and Andersson (1986) is speculative at this stage.

The ability of male elephants to guard oestrous females and obtain copulations during mid-oestrus

increases dramatically late in life. It is possible that female elephants who choose to mate with older males are mating with males who are associated with a higher than average fitness as suggested by Manning (1985). Although it remains to be shown whether factors affecting longevity are heritable, the behaviour of female elephants indicate that they prefer old males and lends support to this hypothesis.

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