



Age, musth and paternity success in wild male African elephants, *Loxodonta africana*

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(Received 21 September 2006; initial acceptance 3 November 2006;
final acceptance 1 December 2006; published online 13 July 2007; MS. number: A10565)

Male African elephants experience intense intrasexual selection in gaining access to oestrous females, who represent a very scarce and highly mobile resource. An unusual combination of behavioural and physiological traits in males probably reflects this intense selection pressure. Males show prolonged growth, growing throughout much or perhaps all of their long life span (ca. 60–65 years), and they show musth, a physiological and behavioural condition exclusive to elephants, which is manifested by bouts of elevated testosterone and aggression and heightened sexual activity. Most observed matings are by males over 35 years of age and in musth, suggesting that age and musth are both important factors contributing to male reproductive success. Here we report the results of a genetic paternity analysis of a well-studied population of wild African elephants. Patterns of paternity for 119 calves born over a 22-year period showed significant effects of both age and musth on paternity success. Among males in musth, paternity success increased significantly with age until the very oldest age classes, when it modestly declined. When not in musth, males experienced relatively constant, low levels of paternity success at all ages. Thus, despite the importance of both musth and age in determining male paternity success, adult males both in and out of musth, and of all ages, produced calves. In general, however, older males had markedly elevated paternity success compared with younger males, suggesting the possibility of sexual selection for longevity in this species.

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Keywords: African elephant; age-related behaviour; competition; dominance status; genetic paternity success; *Loxodonta africana*; male–male conflict; mating; musth

Dominance status is a recurring theme in analyses of male reproduction in many animal taxa. This reflects the fact that in many (but not all) species, access to reproductive females is strongly influenced by male–male competition (Andersson 1994; Ellis 1995). However, males attain their dominance status in different ways. In some species and across a wide range of taxa (e.g. invertebrates, mammals and fish), size alone is a strong predictor of dominance rank, presumably because it is a strong predictor of

fighting ability (Moczek & Emlen 2000; Reichard et al. 2005; Carlini et al. 2006). In other species, other factors, such as physiological state, may contribute to a male's ability to dominate other males. For instance, in some cooperatively breeding species, dominant males may be distinguished from other males by their higher androgen profiles and they may socially and/or physiologically suppress reproduction in subordinates (Clarke & Faulkes 1998; Peters et al. 2001; Bales et al. 2006; Bender et al. 2006). The common theme in all these examples is that males in many taxa have experienced strong selection to dominate other males for reproductive opportunities. This selection pressure has resulted in a diversity of means by which they do so.

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Elephants represent a particularly interesting and unusual example of this diversity. Male elephants face very intense reproductive competition and they show a unique dominance pattern in which individual males repeatedly experience periods of both high and low dominance status. Both the intense reproductive competition that male elephants experience and the distinctive dominance patterns that they show arise from the particular behavioural ecology and life history of elephants. African elephants live in fission–fusion societies in which males and females do not co-reside in permanent social groups. Females live in fluid social groupings generally with their female relatives and calves (Archie et al. 2006), while males range independently of these female groups, joining them only occasionally for brief periods to travel and mate (Moss & Poole 1983; Poole & Moss 1989). Female groups are highly mobile, vary over time in size and composition, and only rarely contain females in oestrus; each adult female is sexually receptive only for 3–6 days every 3–9 years (reviewed in Moss 1983; Poole & Moss 1989). Thus, male elephants face the reproductive challenge of locating very scarce, highly mobile reproductive females, and of preventing other males from gaining access to them (Poole 1989b; Poole & Moss 1989).

Male elephants show an unusual combination of behavioural, morphological and physiological traits that are thought to reflect the intense competition for access to females that they experience (Poole 1989a, b; Poole & Moss 1989; Poole et al., in press). First, they show prolonged and possibly indeterminate growth: they continue to grow in stature, body mass and tusk weight throughout much and possibly all of their life (Roth 1984; Haynes 1991; Lindeque & van Jaarsveld 1993; Lee & Moss 1995). Second, they have a very long life span. Median life expectancy for male elephants in Amboseli is estimated to be 26 years; about 25% of males survive beyond the age of 40 (Poole et al., in press) and males in their 60s are regularly sighted in the population (Lee & Moss 1995; Moss 2001). Male elephants thus have a very long potential life span (ca. 65 years; Haynes 1991). Consequently, the size disparity among reproductively mature males may be very large depending on population demographics. For instance, a 40-year-old male may be twice the weight and 30% taller than a 20-year-old male (Poole et al., in press). Because dominance rank is size dependent, and males grow throughout life, males gain in dominance rank as they age (Poole 1989a).

In addition, healthy adult male elephants show musth, a physiological and behavioural condition that is manifested by bouts of elevated testosterone and aggression, and heightened sexual activity. The importance of musth has been well documented by behavioural observations (Moss 1983; Hall-Martin & van der Walt 1984; Hall-Martin 1987; Poole 1987, 1989a, b, 1999). Males begin to experience musth at a mean of 29 years of age (Poole 1987), and, as a male ages, his musth episodes typically increase in duration throughout his life. Among young males, musth generally lasts for only a few days or weeks, whereas in older males, it typically lasts for several uninterrupted months (Poole 1987, 1989a). Specifically, median duration

of musth increases from 2 days for males aged 16–25 years, to 13 days for males aged 26–35 years, to 52 days for males aged 36–40 years, to 69 days for males aged 41–45, to 81 days for males aged 46–50 years, and then declines again to 54 days for males aged 51–60 years of age (Poole et al., in press). Furthermore, young males experience musth at irregular intervals, but as an individual male ages, his musth periods generally stabilize to an approximately annual occurrence (Poole 1987, 1989a, b; Poole et al., in press). However, musth does not occur synchronously among adult males. Musth may be observed in every month of the year, but relatively few males are in musth concurrently within a population (Poole 1987, 1989a). Being in musth temporarily raises a male's dominance status above males not in musth, including those larger than himself that he would otherwise rank below (Poole 1987, 1989a). Male elephants compete directly and sometimes intensely for access to mates, and even occasionally kill each other; escalated aggressive interactions generally involve a male in musth (Hall-Martin 1987; Poole 1989a). Musth appears to be an energetically costly state to maintain; males lose weight and their physical condition visibly deteriorates as musth progresses (Poole 1989a), presumably because of decreased foraging (Poole 1982) coupled with increased distance travelled (Poole 1982) and alterations in body homeostasis (Schulte & Rasmussen 1999). The oldest males experience the largest deterioration because they maintain musth for the longest periods (Poole 1989a).

Musth also influences the association patterns and sexual behaviour of both male and female elephants. Males in musth range more widely than nonmusth males, spending more time with female groups or alone and less time with other males (Hall-Martin 1987; Poole 1989a; Rasmussen et al. 1996). Female elephants appear to prefer older musth males as mates, maintaining close physical proximity to older males who are in musth when they are in oestrus (Moss 1983). Musth males have higher mate guarding and mating success than nonmusth males. Nonmusth males do show breeding behaviour and mate successfully (Poole 1989b), however, most observed matings are by musth males over 35 years of age (Moss 1983; Poole 1989b).

Here, we addressed two questions using a genetic paternity analysis of the wild population of African elephants living in and around Amboseli National Park, Kenya. First, we tested the hypothesis that the higher mating success experienced by older males in musth (Poole 1989a, b; Poole et al., in press) translated into higher paternity success. Genetic determination of paternity was important because studies in some species have shown that dominance rank, mate guarding and even mating itself are not always good predictors of actual paternity (Pemberton et al. 1992; Hughes 1998; Coltman et al. 1999; Eady & Hardy 2001; Preston et al. 2001). Second, we quantified the impact of both age and musth on male paternity success. Mating success increases markedly with age (Poole 1989b; Poole et al., in press), as does the duration of musth (Poole 1987, 1989a; Poole et al., in press). We developed a model to test the contributions of each to male paternity success.

METHODS

Data Set

The subjects of our study were wild African elephants living in and around Amboseli National Park, Kenya. This population has been continuously studied since 1972 (Moss 2001) and all elephants are individually recognizable based on individual physical characteristics and are habituated to researchers' presence (Moss 2001). Sightings of individuals are done on an opportunistic basis, by a core of five experienced elephant researchers (mean = 19.8 years with the project, range 12–30 years). Life history and behavioural data for the approximately 1300 elephants in the population (including births, deaths, musth, oestrus, mating and mate guarding records), are documented in the Amboseli Elephant Research Project (AERP) databases (Moss 2001).

Every animal in the study population has been assigned an age as part of the ongoing long-term research. Ages for elephants born after 1975, with few exceptions, were known to within ± 2 weeks. Elephants born from 1972 through 1975 were known to within ± 3 months. Ages of individuals born before 1972 were estimated based on validated techniques that have been used in multiple elephant populations (Haynes 1991; Lee & Moss 1995; Moss 2001). Ages of individuals born in 1970–1971 were considered accurate to ± 6 months and those born in 1968–1969 were considered accurate to ± 1 year. The ages of individuals born in 1963–1967 were considered accurate to ± 2.5 years and individuals born before 1963 were considered accurate to ± 5 years. These accuracies are based on known patterns of variance in size measures with increasing age (Haynes 1991; Lindeque & van Jaarsveld 1993; Lee & Moss 1995; Morrison et al. 2005).

Genetic Sampling and Genotyping

Samples from 89 adult male Amboseli elephants (age 17–59 years old) and 279 calves and their mothers were used in the analysis described here. For nearly 85% of all elephants sampled, we obtained multiple faecal samples, collected on separate days (mean = 3.9 samples per individual, range 2–14 samples). For the remaining 15%, we collected a single faecal sample. In addition, a single tissue sample was collected from 58 individuals. DNA was extracted from faeces using a QIAmp DNA Stool Kit (Qiagen) following the methods described in detail by Archie et al. (2003). Tissue DNA was extracted using a DNeasy Tissue Kit (Qiagen, Valencia, California, U.S.A.) following the manufacturer's protocol. PCR products were separated using an ABI PRISM 3700 DNA analyser (Applied Biosystems, Foster City, California) and allele sizes were determined using GENOTYPER 2.0 software (Applied Biosystems).

We genotyped individuals at eight of the microsatellite loci described by Archie et al. (2003): LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18 and LaT24. Loci were amplified as in Archie et al. (2003), and genotypes were assigned using a modified multiple-tubes methods (Taberlet et al. 1996), as described in Archie et al. (2006).

For individuals with multiple samples, we replicated DNA amplification from two samples, either a tissue and a faecal sample or, if tissue was not collected, from two faecal samples collected on separate days. Genotypes for faecal and tissue samples matched for 57 of the 58 individuals for whom we had both. In the one instance where tissue and faeces did not match (mismatched at 5 of 8 loci), we assumed that the mismatch was due to misidentification of a faecal sample in the field, and we used only the tissue sample (see Buchan et al. 2005). To be conservative, we assigned a given allele to a given individual only when it amplified consistently either in a minimum of two reactions with at most one other allele also amplifying (for heterozygous individuals) or in a minimum of seven reactions with no other alleles amplifying (for homozygous individuals). Lastly, we conducted Mendelian checks for all mother–offspring pairs.

The population showed high genetic diversity, with a mean number of alleles per locus of 13.25 (range 9–19); all eight loci provided informative data. All loci were in Hardy–Weinberg equilibrium (CERVUS chi-square: $P < 0.01$) and mean expected heterozygosity was 0.834. The null allele frequency was near zero for all loci (range -0.0141 , $+0.0121$), suggesting that no loci had to be excluded from the analysis because of allele nonamplification resulting from primer-binding-site mutation (Marshall et al. 1998). The mean observed error rate across all loci, calculated by CERVUS, was 0.0082. The cumulative power of exclusion for identifying the second parent when one parent was known was 0.9999.

Paternity Analysis

Putative fathers were identified using CERVUS 2.0 (Marshall et al. 1998). The offspring analysed were conceived over a period of 22 years (1977–1998). Because CERVUS is very sensitive to the proportion of candidate parents sampled (Krützen et al. 2004), and this proportion varied over the 22-year period, we ran different simulations of CERVUS for periods with different proportions of candidate males sampled. We kept the following input parameters constant for all CERVUS simulations: 10 000 cycles, 90 candidate parents, 100% of loci typed, 1% of loci mistyped and confidence levels of 95% strict and 80% relaxed. However, we varied the value for the proportion of candidate males sampled depending upon conception years: 33% (1977–1980), 45% (1981–1985), 55% (1986–1990), 61% (1991–1995) and 74% (1996–1998). This procedure resulted in paternity assignments with 95% confidence for 119 calves. For most calves ($N = 114$), the assigned male was the only male who had zero mismatches with the offspring (i.e. all other adult males had one or more mismatches). In the other five cases, the assigned male mismatched at a single homozygous locus ($N = 4$) or at two homozygous loci ($N = 1$). These 119 calves represented approximately 10% of recorded births in the entire population during the study years (Table 1). Most of the calves for whom fathers were not assigned were from earlier years of the study, for which fewer mothers were sampled and smaller

Table 1. Distribution of elephant offspring births recorded in the study population by year and number of assigned paternities

Birth year	Recorded number of offspring born	Number of confirmed paternities	Percentage of assigned paternities
1978	5	1	20
1979	57	3	5
1980	53	2	4
1981	25	1	4
1982	33	0	0
1983	82	2	2
1984	40	0	0
1985	61	4	7
1986	24	1	4
1987	66	7	11
1988	40	3	8
1989	28	0	0
1990	49	6	12
1991	74	10	14
1992	39	4	10
1993	35	7	20
1994	64	5	8
1995	71	9	13
1996	74	8	11
1997	53	8	15
1998	35	6	17
1999	116	13	11
2000	114	19	17
Total	1238	119	10

proportions of candidate fathers were sampled. However, other than their year of birth, there was no obvious source of bias (e.g. based on maternal home range or natal family group) in the set of calves for which we were able to assign paternity, so that these 119 calves should represent a random sample of calves drawn from the population.

Analysis of Age and Musth Effects

To examine the effects of age on paternity success, we designated male age classes using 1-year intervals (e.g. the 40-year-old age class comprised all males in their 40th year, etc). We then calculated the number of offspring produced per opportunity by adult males in each class age (17 years and older). First, we assigned each offspring to a male age class depending upon the age of the father at that offspring's conception. Next, we counted the number of opportunities that males in each age class had to father offspring, by counting the number of adult males alive in the population in each age class at the time of each opportunity for paternity (each male had one opportunity for each conception). Owing to maturation and death, the number of adult males in each age class changed for each year of the study. Then, to get the number of offspring produced per opportunity by males in each age class, we divided the total number of offspring produced by males in each age class by the number of opportunities that males had in those age classes (again, counting one opportunity for each genotyped male that was present in the population at the time of that conception).

Each calf matched to a genotyped male in our study represented an opportunity for the genotyped males to

produce an offspring. For example, we calculated age-specific paternity success at age 45 by first counting the number of offspring matched to males of age 45 ($N = 8$; one calf conceived in 1985, three in 1990, two in 1995, and one calf each in 1996 and 1998). Then we calculated the number of opportunities to produce offspring by males age 45 by summing, over all years, the number of calves assigned paternity multiplied by the number of males that were age 45 that year. In 1989, for example, one male was age 45 and six calves were assigned paternity; therefore, 45-year-old males had six opportunities to sire calves that year. In 1990, two males were age 45 and nine calves were assigned paternity (2×9). Thus, there were 18 opportunities for 45-year-old males to sire calves in 1990. We defined the paternity success for each age class as the number of offspring produced by males of that age class, divided by the total number of opportunities for conceiving calves by males of that age class pooled across all years of the study.

To highlight the major age-related trends and minimize the effects of noise in the data, we generated a smoothed curve (with 95% confidence intervals) by using a 10-year moving average, for yearly intervals beginning with age 21.5 years. That is, the average number of offspring per opportunity for age 21.5 years was generated by taking the total number of calves assigned to males for ages 17 through 26 years divided by the opportunities for the males aged 17 through 26 years; the average for age 22.5 years was generated by summing the values for ages 18 through 27 years, and so on through age 54.5 years (the last age for which we could take a 10-year average).

We examined the effects of musth on age-specific paternity success by examining the musth records of each assigned father and all genotyped nonfathers during the month that each offspring was presumed to have been conceived (defined as 22 months before the recorded birth month; Moss 1983). Males were considered to be in musth if they showed secretions from swollen temporal glands with facial staining and concurrent urine dribbling or the evidence of recent dribbling (e.g. urine stains on the inside of the legs; Poole 1987). We assigned fathers to the 'in musth' as opposed to the 'not known to be in musth' category only if they were unambiguously seen in musth during the month that conception was presumed to occur. This was a highly conservative approach because males in musth may not be seen by observers in a given month because of their protracted movement patterns and the relatively large size of the population. Consequently, this approach resulted in assigning a number of fathers to the 'not known to be in musth' state that were probably in musth at the time of conception, but were not seen by observers; for instance, if a male was seen in musth during the month before the presumed conception date and during the month after the presumed conception date, but was not seen during the month of the presumed conception, we conservatively assigned him to the 'not known to be in musth' category. We then used a chi-square test to assess statistically whether fathers were more likely to be in musth than nonfathers.

For a subset of conceptions ($N = 56$), the mother was observed during oestrus. We used these behavioural

records, which included records of female oestrous behaviour and male mate guarding and mounting, to examine the effects of musth during the week of conception for these 56 conceptions. Females were considered in oestrus if, in the presence of males, they showed wariness, 'oestrous walk', chase, mount and consort behaviours, as described in Moss (1983).

Modelling

We developed a model to describe the relationship between paternity success and age and musth in Amboseli elephants. Our model for paternity success models the probability of a male siring a calf given the male's age and musth status in the month that the calf was conceived. Our model computes the probability of siring each calf for all the adult genotyped Amboseli males alive at that conception. Using the R statistical package v 2.2.1 (The R Foundation, Vienna, Austria), we performed a logistic regression for males $i = 1, \dots, 89$, and calves $j = 1, \dots, 119$.

$$\begin{aligned} \text{logit}(p_{ij}) &= \log(p_{ij}/1 - p_{ij}) \\ &= \beta_0 + \beta_1 + \beta_1 \text{Age}_{ij} + \beta_2 \text{Age}_{ij}^2 + \beta_3 \text{Musth}_{ij} \end{aligned}$$

where Age_{ij} is the age of male i at the time of conception of calf j , and $\text{Musth}_{ij} = 0$ if male i was not seen in musth during the month of conception of calf j , but $\text{Musth}_{ij} = 1$ if male i was seen in musth during the month of conception of calf j . These variables then determine p_{ij} , the probability that male i sired calf j . We determined the P values of the parameter estimates to identify whether the terms in the model accounted for significant variance in the data.

Like all statistical models, this model contained some false assumptions. In particular, the model implicitly assumed that a male's paternity success was independent from one year to the next, an assumption that was almost certainly incorrect, as some males were clearly better reproducers overall than others. However, the effects of this false assumption on our conclusions were probably very minor; no single male or small subset of males contributed disproportionately to the data set (see Fig. 1), and both age and musth produced overwhelmingly strong effects in the model, an effect that could not be due to pseudoreplication in this data set (see Results).

RESULTS

Males varied greatly in the number of offspring they produced, and in the ages at which they produced them (Fig. 1). Thirty-six males, somewhat less than half of the genotyped Amboseli males over the age of 25, fathered the 119 genotyped offspring in our analysis. Just three males were responsible for 36 (30%) of the 119 assigned paternities. These three males, each of which fathered 12 calves in our analysis, also had the highest guarding and mating success in our behavioural records of oestrus and mating, supporting our hypothesis that mating success would predict paternity success in this population. These

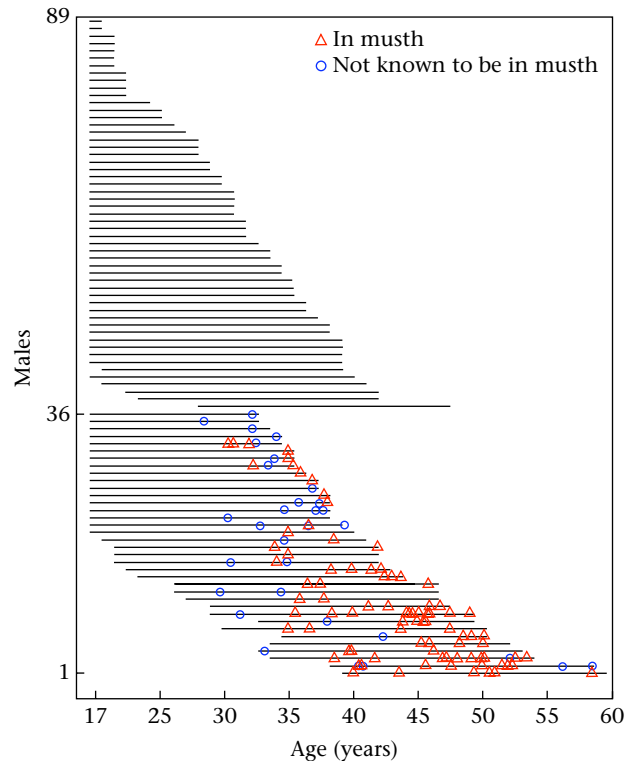


Figure 1. Life history data for the 89 genotyped male African elephants in this study. Each line represents the known life history of one of the 89 males in the sample. Lines in the upper half of the plot represent genotyped males that fathered no offspring in our data set. The plot shows the distribution of age ranges that we were able to analyse for each male and the cross-sectional nature of the data set; for some males, we captured the early part of the life history; for others, we captured the later part of the life history. Each symbol represents a reproductive event (a calf conceived) while the male was in musth (Δ) or not known to be in musth (\circ).

males were also among the oldest genotyped males in the population in 1998, at 58, 53 and 48 years old. However, males sired offspring beginning in young adulthood (the youngest father in our data set was 26 years old at the time that he conceived the calf), indicating that paternity success was not strictly age dependent.

Age and Paternity Success

The youngest and oldest males for whom we documented paternity were 26 and 59 years old, respectively, at the time of calf conception. Although males as young as their mid-20s sired offspring, this was not a common event; six males sired a total of eight calves among them during their 20s (Hollister-Smith 2005). Age-specific paternity success, as measured by the number of calves fathered per opportunity at a given age, increased steadily from the mid-20s until a peak between 45 and 53 years of age (Fig. 2). Paternity success then declined to levels comparable to a male in his early 40s. Siring offspring in old age was not a rare occurrence. Four males sired 14 calves among them when they were in their 50s.

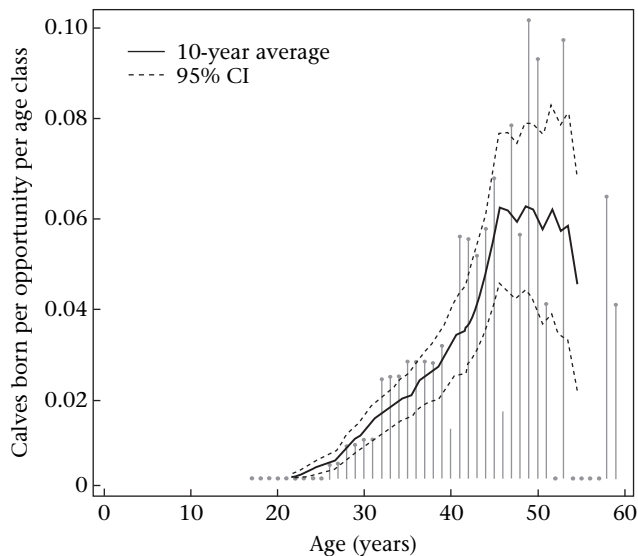


Figure 2. The relationship between male age and paternity success in African elephants, using data from 89 genotyped Amboseli males and 119 calves for whom we assigned paternity. The vertical lines denote the number of offspring produced per siring opportunity by males of each age in Amboseli. To highlight the major age-related trends, the solid line represents a smoothed curve (with 95% confidence intervals) generated by using a 10-year moving average of age for yearly intervals (see [Methods](#)).

Musth and Paternity Success

Musth males had much higher paternity success than expected, based on the frequency of musth males in the population at the time of conceptions. Specifically, 74% (88/119) of the calves were fathered by males known to be in musth and 26% of the calves were fathered by males not known to be in musth. This was quite different from the relative frequencies of musth and nonmusth males in the population; only 12.7% of all genotyped males were in musth during conception opportunities (1066 males in musth versus 7312 males not known to be in musth pooled over the 119 conceptions; each adult male in the population at the time of each conception was counted once, in musth or not known to be in musth, for each conception). This difference between the paternity success of musth and nonmusth males was highly significant ($\chi^2_1 = 401.9, P \ll 0.0001$).

These striking effects of musth appeared in our data even with our highly conservative manner of assigning musth status, in which any males not known with certainty to be in musth were assigned as ‘not known to be in musth’. Consequently, it is very likely that our estimate of the number of conceptions attributed to fathers in musth was an underestimate (see [Methods](#)). This is especially true given that most conceptions to fathers not known to be in musth involved younger fathers. Younger males typically stay in musth for much shorter periods, increasing the probability that we would not have detected them in musth. Hence, we conclude that the difference we have documented in the number of calves fathered by musth versus nonmusth males represents a minimum difference. This is supported by our

data for the subset of 56 calves with known conception dates. For these calves, behavioural records of mothers’ oestrus were available (see [Methods](#)), increasing the probability that we observed the father at the time of conception. In this subset, the proportion of fathers in musth at conception was 79%. Taken together, these results suggested that musth had an enormous impact in determining male paternity success, and led us to investigate the importance of age and musth jointly in a formal model.

Modelling Effects of Age and Musth on Male Paternity Success

Our model illustrates the conspicuous effects of age and musth on male paternity success (logistic regression: $\chi^2_3 = 279.72, P \ll 0.0001$; [Table 2](#), [Fig. 3](#)). Both linear and second-order effects of age were statistically significant ([Table 2](#)). Still more striking was the manner in which musth contributed to paternity success. In particular, in the absence of musth, age contributed relatively little to variance in paternity success, because males not in musth experienced relatively constant, low levels of success at all ages. However, age did strongly contribute to the paternity success of musth males ([Fig. 3](#)). Thus, a 45-year-old male in musth is predicted to outcompete a 25-year-old male in musth. However, a male in musth in his mid-20s experiences a measurable advantage over his agetates that are not in musth; he is predicted to achieve approximately the same paternity success as a 50-year-old nonmusth male.

DISCUSSION

Our analyses indicate that two factors profoundly affected the paternity success of male elephants. First, male paternity success increased with age until late in life. Second, most calves were sired by males who were in musth at the time of calf conception. The first result supports the observation that age predicts a male’s position in the male dominance hierarchy, and that older males are able to outcompete younger males for access to females ([Poole 1989b](#); [Poole et al., in press](#)). In contrast to age, which represents a dominance queue, musth appears to allow a male to ‘jump the queue’ of the age/size dominance hierarchy; musth males can outrank nonmusth males ([Poole 1989a](#); [Poole et al., in press](#)), and because musth occurs asynchronously, unlike a seasonal rutting period, adult males of all ages reproductively contribute

Table 2. Results of logistic regression model for the effects of age and musth on paternity success in male African elephants

Predictor variable	Estimate	Standard error of estimate	Z	P
Intercept	-13.67	2.07	-6.61	$\ll 0.0001$
Age	0.395	0.105	3.778	0.0002
Age ²	-0.004	0.001	-3.259	0.001
Musth	2.306	0.227	10.154	$\ll 0.0001$

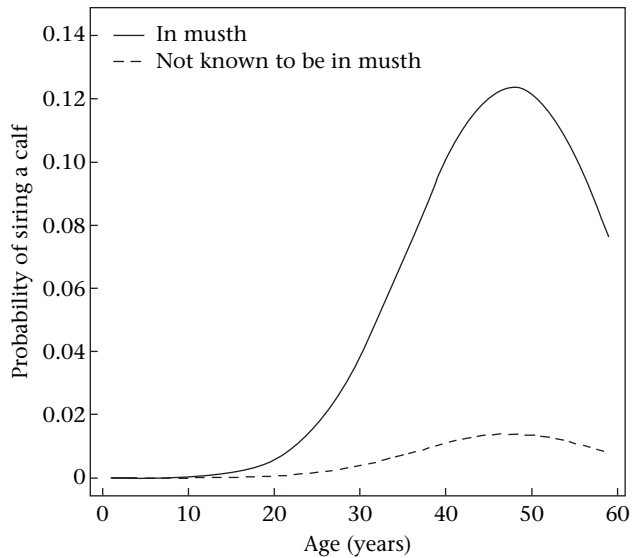


Figure 3. Model predictions for the relationship between paternity success and age and musth in male African elephants. Curves were generated using the parameter estimates described in Table 2. See Methods for details.

to the population. Musth does not annul the hierarchy, however.

Older musth males had a marked advantage over younger musth males (Fig. 3). The effect of musth was more dramatic for older males, in part, because older males in musth are dominant over younger males in musth as well as over all males not in musth. In contrast, younger musth males are lower ranking than older males in musth, even though they can outrank males not in musth. This situation ultimately reinforces the reproductive dominance of older males, so that reproductive success increases dramatically with age for musth males until late in life. Older males are also able to remain in musth longer than younger males (Poole 1987, 1989a; Poole et al., in press), and this effect also reinforces the reproductive dominance of older males. In particular, males between 45 and 50 years of age produced calves at an average annual rate six times that of 30-year-old males (Fig. 2). This finding suggests that male elephants may experience sexual selection for longevity (Poole 1989a, b; Poole et al. in press). However, relatively few males in the population lived to 50 years, and survival to 50 years is estimated at less than 10% for males (Moss 2001; Poole et al., in press).

In spite of the reproductive superiority of older musth males, younger males' reproductive contribution was not inconsequential. Indeed, males under 35 years of age fathered 29% of the offspring in the study. Several factors probably contribute to younger males obtaining matings. Because elephants do not live in permanent male–female associations and females enter oestrus only rarely, musth males may not be immediately available when a female enters oestrus. Males must find oestrous females through a protracted and intensive searching effort (Poole & Moss 1989). Females may suffer reproductive costs (e.g. nonconceptive cycles) if they do not mate with available males during their brief oestrus. Moreover, even young adult

males are larger than most adult females (Lee & Moss 1995), so it may be physically difficult for a female to resist mating attempts. Females actively attempt to evade advances by young males (Moss 1983), however, they are frequently harassed by multiple males during oestrus if they are not guarded by a larger, older musth male (Moss 1983; Poole 1989b). Younger males may also have the advantage of sneaking mating opportunities when older males interact with each other (Poole 1989b). Finally, although females in general appear to prefer large musth males, female preferences may be idiosyncratic to some extent, possibly reflecting preferences for males with whom they are particularly compatible regardless of age or size (see review in Neff & Pitcher 2005).

This pattern of continued high male reproductive output into old age is unlike that of most described mammalian species (Table 3; e.g. baboons, *Papio cynocephalus* (Alberts et al. 2003, 2006), rhesus macaques, *Macaca mulatta* (Bercovitch et al. 2003), red deer, *Cervus elaphus* (Clutton-Brock et al. 1988), northern elephant seals, *Mirounga angustirostris* (Le Boeuf & Reiter 1988), fallow deer, *Dama dama* (McElligott & Hayden 2000; McElligott et al. 2002), greater kudu, *Tragelaphus strepsiceros* (Owen-Smith 1993), lions, *Panthera leo* (Packer et al. 1988), and chimpanzees, *Pan troglodytes* (Boesch et al. 2006)). Typically, the reproductive output of a male mammal peaks when he reaches his full adult body size, which occurs soon after he achieves sexual maturity. At this point males are usually in their peak physical condition and at their highest dominance rank. Males often maintain high dominance rank for a relatively short period, perhaps only one or a few breeding seasons. As body condition deteriorates and they can no longer compete with younger males, reproductive performance of many male mammals steadily declines. For most male mammals, peak reproductive output is achieved within the first half of the total adult life span (Clutton-Brock et al. 1988; Le Boeuf & Reiter 1988; Packer et al. 1988; Owen-Smith 1993; McElligott & Hayden 2000; McElligott et al. 2002; Alberts et al. 2003, 2006; Bercovitch et al. 2003; Boesch et al. 2006). The consequence is that male breeding life span is compressed into a fraction of its full potential because of intense competition from other males (Clutton-Brock 1988).

Male elephants appear to represent the extreme among mammals in the extent to which they show high mating and paternity success until late in life. Two noteworthy features of elephant physiology and behaviour are probably responsible for this: (1) male elephants continue to grow throughout much or all of life (Roth 1984; Haynes 1991; Lindeque & van Jaarsveld 1993; Lee & Moss 1995), and (2) older males maintain musth longer than younger males (Poole 1987). The prolonged growth experienced by male elephants may be a key factor accounting for the increase in age-specific paternity success demonstrated here. For many organisms, size is more important than age in determining life history parameters (Kirkpatrick 1984). Size is probably a major contributor to the ability of older male elephants (with higher body mass and thus potentially higher energy reserves) to sustain musth longer than smaller males. Because of continued growth, a male elephant may actually increase his

Table 3. Age at which peak male reproductive output occurs relative to life span in various mammals

Species	Age at peak reproductive output (years)	Life span (years)*	Age at maturity (years)†	Study length (years)	Number of males in study	Peak at		Source
						% Total life span‡	% Adult life span§	
Macaques, <i>Macaca mulatta</i>	7.5	24	3.5	10	364	31	17	Bercovitch et al. 2003
Baboons, <i>Papio cynocephalus</i>	9	22	6	12	115	41	19	Alberts et al. 2003, 2006
Fallow deer, <i>Dama dama</i>	7	13	3.5	15	318	54	36	McElligott & Hayden 2000; McElligott et al. 2002
Lions, <i>Panthera leo</i>	8	14	3.5	~10	91	57	43	Packer et al. 1988; Nowak 1999†
Chimpanzee, <i>Pan troglodytes</i>	22	50	9	14	9	44	46	Boesch et al. 2006
Kudu, <i>Tragelaphus strepsiceros</i>	6	9	3	6	Unknown	67	50	Owen-Smith 1993
Red deer, <i>Cervus elaphus</i>	8.5	13	2.5	7	33	65	57	Clutton-Brock et al. 1988; Nowak 1999†
Elephant seals, <i>Mirounga angustirostris</i>	10	14	4.5	16	138	71	58	Le Boeuf & Reiter 1988
African elephants, <i>Loxodonta africana</i>	49 (midpoint of 45–53)	62.5	15.5	22	89	78	71	This study

Species are listed from the earliest to the latest age at which peak reproductive output occurs relative to adult life span.

*Life span is the upper limit for the species, as listed for the study population.

†Age at maturity is the estimated age at physical maturity (not social maturity) given for the study species, except for lions and red deer, for which the source did not state an age at physical maturity. We obtained the age at physical maturity for lions and red deer from Nowak (1999).

‡Age at which peak reproductive output occurs/life span.

§(Age at which peak reproductive output occurs – age of maturity)/(life span – age of maturity).

physical vigour for several decades as he ages rather than show the typical decline. Musth and prolonged growth contribute to two other unusual aspects of elephant behaviour. First, because male elephants repeatedly enter musth, they repeatedly rotate into and out of high dominance in a population throughout their adult life span (Poole 1989a). We know of no other mammalian system that functions in this manner. Second, older males appear able, on occasion, to influence the length of musth in younger/smaller males (Poole 1989a; Slotow et al. 2000), suggesting social suppression of reproduction and a further advantage to age and the large body size that goes with it.

Elephants are unusual among mammals, but Weilgart and colleagues have proposed that cetaceans, and particularly sperm whales, *Physeter macrocephalus*, may be convergent with elephants in some aspects of reproductive behaviour (Weilgart et al. 1996; Whitehead 2003). Parallels between these two evolutionarily distant species include complex social organizations, large brains and exceptionally slow life histories (long life spans, late maturation, low adult mortality, excluding anthropogenic causes, and long interbirth intervals). In addition, in both species, related females live in spatially fluid multi-generational groups composed of several hierarchical levels, males continue to grow long after reaching sexual maturation, and roving males show an age-delayed competitive breeding strategy (Whitehead 1994, Whitehead & Weilgart 2000). It is not known whether anything like musth, with its associated fluctuations in dominance status, occurs in whales. Unfortunately, although not

surprisingly given the difficulties of whale research, data to determine this are currently lacking (Whitehead 2003).

It is difficult to know whether indeterminate growth in male elephants is the result of sexual selection for size in this species, or whether indeterminate growth evolved for other reasons. The pattern of repeatedly entering musth suggests repeated switching by individual males between allocation to growth and allocation to reproduction, with the balance slowly shifting to reproductive output (Poole 1989a) until an advanced age, when erosion of the sixth and final set of molars (Haynes 1991) may compromise a male's ability to replenish body weight during nonmusth periods. Heino & Kaitala (1999) propose that indeterminate growth may result from such a seasonal switching in other systems.

Acknowledgments

We thank the Office of the President of the Republic of Kenya and the Kenya Wildlife Service for permission to work in Amboseli. We also thank the Wardens and staff of Amboseli National Park and the pastoralist community of Amboseli for continuous cooperation and assistance. Members of the Amboseli Elephant Research Project provided scientific and logistical support, particularly S. Sayialel, N. Njiraini and K. Sayialel. L. Bukovnik provided technical assistance with microsatellite analysis at Duke University. We thank M. Lavine of the Institute of Statistics and Decisions Sciences at Duke University for statistical advice. This work was supported by the National

Science Foundation (IBN0091612 to S.C.A.), the African Elephant Conservation Trust and the Amboseli Elephant Research Project. All protocols complied with relevant regulations in Kenya (Kenya Research Permit MOES&T 13/001/30C 72/7) and the U.S. (Duke University IACUC protocol A436-00-09).

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