

Age- and tactic-related paternity success in male African elephants

H.B. Rasmussen,^{a,b,c} J.B.A. Okello,^d G. Wittemyer,^{c,e} H.R. Siegismund,^b P. Arctander,^b F. Vollrath,^{a,c} and I. Douglas-Hamilton^c

^aAnimal Behaviour Research Group, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK, ^bEvolutionary Biology, Department of Biology, University of Copenhagen, Universitetsparken 15 DK-2100 Copenhagen Ø, Denmark, ^cSave the Elephants, P.O. Box 54667, 00200 Nairobi, Kenya, ^dMolecular Biology Laboratory, Makerere University Institute of Environment & Natural Resources, P.O. Box 7298, Kampala, Uganda, and ^eDepartment of Environmental Science, Policy and Management, University of California at Berkeley, 201 Wellman Hall, Berkeley, CA 94720, USA

Information on age- and tactic-related paternity success is essential for understanding the lifetime reproductive strategy of males and constitutes an important component of the fitness trade-offs that shape the life-history traits of a species. The degree of reproductive skew impacts the genetic structure of a population and should be considered when developing conservation strategies for threatened species. The behavior and genetic structure of species with large reproductive skew may be disproportionately impacted by anthropogenic actions affecting reproductively dominant individuals. Our results on age- and tactic-specific paternity success in male African elephants are the first from a free-ranging population and demonstrate that paternity success increases dramatically with age, with the small number of older bulls in the competitive state of musth being the most successful sires. However, nonmusth males sired 20% of genotyped calves, and 60% of mature bulls (>20 years old) were estimated to have sired offspring during the 5-year study period. The 3 most successful males sired less than 20% of the genotyped offspring. Hence, contrary to prediction from behavior and life-history traits, reproduction was not heavily skewed compared with many other mammalian systems with a similar breeding system. Nevertheless, these results indicate that trophy hunting and ivory poaching, both of which target older bulls, may have substantial behavioral and genetic effects on elephant populations. In addition, these results are critical to the current debate on methods for managing and controlling increasing populations of this species. *Key words*: Elephants, musth, paternity, reproductive strategy, skew, tactic. [*Behav Ecol* 19:9–15 (2008)]

Age- and tactic-specific paternity success and the degree to which males can monopolize breeding are fundamental factors that influence lifetime reproductive decisions of individual males (Emlen and Oring 1977; Clutton-Brock and Harvey 1978; Rubenstein 1980; Clutton-Brock 1989) and impact population genetic processes (Sugg et al. 1996). In combination with survival, fitness trade-offs driven by age- or tactic-related paternity success are expected to shape life-history traits such as lifespan, time of maturation, growth (Stearns 1992), and potential shifts between alternative reproductive tactics (ARTs) (Whitehead 1994). Therefore, obtaining information on paternity success is pivotal in order to understand both the evolutionary forces that have shaped morphology and life history as well as the short-term optimization processes affecting behavior and the often reversible shifts between ARTs. In this study, we test predictions, based on behavior and life-history traits, of age- and tactic-related reproductive success in male African elephant using genetic analysis of paternity success in a wild population of individually known elephants.

Unlike maternal success, paternity success is not directly observable. Therefore, proxy measures such as the number of matings, mate guarding, and dominance are often used as substitutes. Use of proxy measures is, however, problematic.

Genetic studies in multiple systems have revealed that such proxy measures of paternal success are not always accurate measures of actual success with both under- and overestimates being found, for example, in red deer, *Cervus elaphus* (Pemberton et al. 1992); gray seals, *Halichoerus grypus* (Amos et al. 1993); and Soay sheep, *Ovis aries* (Coltun et al. 1999). An individual's success in siring offspring is determined by the outcome of multiple processes at times acting simultaneously. The successful sire may be determined via overt male–male competition, with the outcome based on physical strength and weaponry, or via covert sperm competition (Preston et al. 2003). It may also be influenced by the male's ability to detect and gain access to mating at the right time relative to female ovulation, which may be partly or exclusively determined by female choice of partner. Using proxy measures for assessing paternity success may be problematic when sperm competition or timing of mating plays a major role in determining the outcome. This may be especially the case in multimale and promiscuous mating systems.

Male African elephants have life-history traits of longevity, indeterminate growth, and large sexual dimorphism (Laws et al. 1975; Lee and Moss 1995; Sukumar 2003), suggesting a high degree of size-dependent competition for mates, favoring larger, older individuals (Maynard-Smith and Brown 1986). Not surprisingly, dominance rank and fighting success are largely determined by size and, therefore, age (Poole 1987, 1989a, 1989b), suggesting increased paternity success with age. Both sexes of elephants are promiscuous with males supplying no parental care (Sukumar 2003). Males are generally regarded as having a rover mating strategy with short-term defense of individual estrous females (Barnes 1982). This strategy is probably

Address correspondence to H.B. Rasmussen, Department of Evolutionary Biology, University of Copenhagen, Universitetsparken 15 DK-2100 Copenhagen Ø, Denmark. E-mail: hebrasrussen@bi.ku.dk.

Received 11 August 2006; revised 11 September 2007; accepted 13 September 2007.

due to the low frequency and unpredictable occurrence of receptive females (Clutton-Brock 1989), which in most populations can occur throughout the year (Laws et al. 1975; Hall-Martin 1987; Poole and Moss 1989). After the age of 30 years, males start engaging in a competitive reproductive tactic known as musth (Poole and Moss 1981) that increases in duration with age (Poole 1987). Musth has been likened to the rutting behavior of ungulates (Jainudeen et al. 1972) and is a complex phenomenon associated with multiple changes in behavior, physical appearance, and physiology. Musth bulls have conspicuous signals like urine dribbling and temporal gland secretion (Poole 1987; Kahl and Armstrong 2002). These signals are considered to be honest signals of dominance and aggressive intent (Poole 1989a), likely linked to the highly elevated androgen levels of musth bulls (Poole et al. 1984; Rasmussen et al. 1984; Ganswindt et al. 2005). Mate guarding is almost exclusively done by musth males, and behavioral observations show that a large fraction of mountings can be attributed to older males in musth (Poole 1987, 1989a, 1989b). Musth males walk more and forage less probably as a result of increased search effort for female (Poole 1987; Rasmussen 2005). Likewise, the majority of fights, sometimes leading to injury and death, are initiated by musth males (Hall-Martin 1987). In addition to the higher male–male dominance rank of musth males, there is evidence for female choice of musth males (Moss 1983; Poole 1987). Females are more likely to outrun younger or lower ranking nonmusth males and thereby avoid mountings and to actively solicit guarding by musth males. Before the present study, the combination of life-history traits, male behavior, and potential female choice has led to the assumption that males do not sire offspring before they start exhibiting musth and that the few older musth bulls are responsible for almost all reproduction (Moss and Poole 1983, 1989b, 1994; Sukumar 2003). As a result, paternity in elephants is predicted to be highly skewed.

Musth may not be the only reproductive tactic in elephants. After puberty (approximately 15 years) and before the onset of regular musth periods (approximately 35 years), bulls are known to mate and have viable sperm (Barnes 1982; JoGayle et al. 1984; Hall-Martin 1987), though they rarely engage in aggressive interactions with competitors and seldom mate guard receptive females (Poole 1989b). These younger bulls may be opportunist breeders or engage in distinct alternative “nonmusth” reproductive tactics. Indeed, a paternity study from a small fenced elephant population, containing 320 individuals inhabiting 103 km² (Whitehouse and Schoeman 2003), found that the dominant musth bull did not monopolize reproduction (Whitehouse and Harley 2002). Unfortunately, low genetic variability and the confined nature of the population limited the conclusions that could be drawn from the study.

ARTs are seen in most taxa including fish (Oliveira et al. 2001; Uglem et al. 2002), reptiles (Moore et al. 1998; Wikelski et al. 2004), and birds (Wingfield 1984). ARTs are widespread in ungulates (Isvaran 2005) and mostly maintained as condition-dependent tactics affected by age, body size, and physical condition. Although a high gain/high cost, competitive reproductive tactic is not predicted to pay before late in life in roving males, younger males may still invest in a low-risk, noncompetitive tactic (Whitehead 1994). ARTs are often less conspicuous and may have gone largely unnoticed in elephants but may contribute relatively large proportions of offspring as seen in, for example, bighorn sheep, *Ovis canadensis* (Hogg and Forbes 1997), and predicted in Antarctic fur seal, *Arctocephalus gazelle* (Gemmell et al. 2001).

The degree of reproductive skew can have implications for conservation and management of a species. High skew will reduce the effective population size of a population (Wright

1938), a concern for small fragmented populations. Because older African elephant males are the preferred targets of both legal trophy hunting and illegal poaching for ivory, the removal of older bulls is likely to have genetic effects and to behaviorally impact the reproductive tactics of younger males (Slotow et al. 2000). Hence, in addition to testing the predicted link between life-history traits and age-related paternity success in this species, information on paternity success is salient for understanding the genetic structure of this keystone species as well as potential genetic and behavioral consequences of changes in population size and age structure.

Here, we evaluate the age- and tactic-specific paternity success among free-ranging, male African elephants and assess the degree of reproductive skew occurring in a natural population. We test the hypotheses that 1) paternity success increases throughout life, with reproductive success being heavily skewed toward few older individuals as suggested by life-history traits in this species and 2) males do not reproduce before the onset of musth as suggested by observational data. Genetic paternity analysis was conducted using microsatellite markers and related to behavioral observations of the reproductive tactics of known individuals.

METHODS

Study population and sampled individuals

The study population inhabits the region in and around Samburu and Buffalo Springs National Reserves in northern Kenya and consists of approximately 900 individuals (150 bulls and 220 breeding females and their calves) that have been individually identified and are closely monitored (Wittemyer 2001; Wittemyer et al. 2005). The ages of all identified individuals were determined from physical characteristics (Moss 2001) to within ± 3 years (Rasmussen et al. 2005). This population is free ranging and part of the larger Laikipia/Samburu population estimated at 5400 individuals (Omondi et al. 2002). The population went through a period of significant poaching during the 1970s (Poole et al. 1992), during which the majority of older bulls were probably killed. The population still loses mature males via illegal killing (Wittemyer et al. 2005), but the age structure of bulls at present does not deviate much from a natural age structure although it lacks very old males 55 years and older. In the study population, 27% (22 individuals) of the 83 regular occurring males (see below for definition) were older than 30 years at the time of the study and bulls in musth above 35 years are continually present during the 2 annual breeding peaks (Rasmussen et al. 2006).

A total of 322 calves were born in the study population between 1998 and 2002 and thus were sired from 1996 to 2000, as estimated from the 22-month gestation period of elephants. Samples for genetic analysis were obtained from 79 calves (25%) and 66 of their mothers (83%). We genotyped 88 (51%) of the 174 identified males in the study population, including living males and those which died during the study. The group of identified males uses the core study area to varying degrees. In order to compare paternity success among males with approximately equal “time effort” directed toward the identified females, males that were observed multiple times per month in at least 4 months of the year within the reserves during both the 2 (per annum) breeding seasons (Rasmussen et al. 2006) were categorized as regularly observed males ($N = 83$). These males were used for comparing relative paternity success as described below. The remaining males were categorized as sporadically observed ($N = 91$)

Table 1
The number of sampled and unsampled males among regularly and sporadically observed males

Total number of identified males (including deceased), 174

Regular observed males, 83				Sporadic observed males, 91			
Above 20 years, 53		Below 20 years, 30		Above 20 years, 62		Below 20 years, 29	
Sampled	Unsampled	Sampled	Unsampled	Sampled	Unsampled	Sampled	Unsampled
27	26	21	9	21	41	19	10

(Table 1). The age structure in 1998 of the regularly occurring males is shown in Figure 1A.

Behavioral observations

Behavioral data on individuals were collected as part of the long-term monitoring program in Samburu. When male elephants were encountered during daily monitoring routes (Wittemyer 2001), they were identified along with associating adult individuals as well as time, position, and the degree of temporal gland swelling, temporal gland secretion, and urine dribbling (following the definitions by Poole (1987). Urine dribbling is the signal most closely associated with increased androgen levels and the aggressive musth tactic (Ganswindt et al. 2005) and was used for defining if a bull was in musth at the time of observation.

Sampling and genotyping

Fresh dung samples (epithelial cells-laden mucosal portions) were collected for genetic analysis immediately after defecation by known individuals. Genetic analysis was based on 20 highly polymorphic microsatellite loci (11 tetranucleotide and 9 dinucleotide loci). Polymerase chain reaction and genotyping protocols for the samples and microsatellites used in the present study have been reported in detail previously (Okello et al. 2005). Each individual locus was genotyped at least twice to confirm the genotypes. For the few inconsistent heterozygotes, genotyping was repeated twice more with the majority genotype used in subsequent analysis. As reported in this previous study, genotyping errors were estimated at 2.5% and null allele rates ranged between 0 and 0.04 across loci, well below levels that could cause underestimation of average exclusion probability (Dakin and Avise 2004).

Paternity assignment

A total of 88 bulls and 79 calves were successfully genotyped for paternity analysis. Paternity assignment using the 79 calves and 88 bulls genotyped was based on 3 approaches: 1) maximum-likelihood assignment of paternity (Marshall et al. 1998), 2) exclusion based on number of incompatibilities (Morin et al. 1994), and finally 3) calculation of relatedness between the assigned father and mother of the calf to evaluate if the candidate father/calf shared maternal inheritance, influencing the likelihood-based assignment (Marshall et al. 1998).

Using the program Cervus 2.0 (Marshall et al. 1998), the 2 most likely fathers were assigned based on maximum likelihood. This program calculates the log-likelihood ratio (LOD) between the likelihood of a candidate father siring the offspring and that of an average random male from a “population” of simulated genotypes. The significance of the

ratio of LOD scores between the 2 most likely candidates (Δ score = $LOD_1 - LOD_2$) cannot be obtained analytically but is based on the simulated results from a large number of parent/offspring combinations using the population level allele frequencies. The following parameters were used for the simulation to obtain critical delta values: proportion loci typed = 0.95, proportion loci mistyped = 0.02 (corresponding to genotyping results calculated from the same genetic dataset, Okello et al. 2005); simulation cycles = 50 000; strict confidence level (95%) and relaxed confidence level (80%); and the number of candidate fathers = 80 (equivalent to the number of live regularly occurring males older than 20 years at the

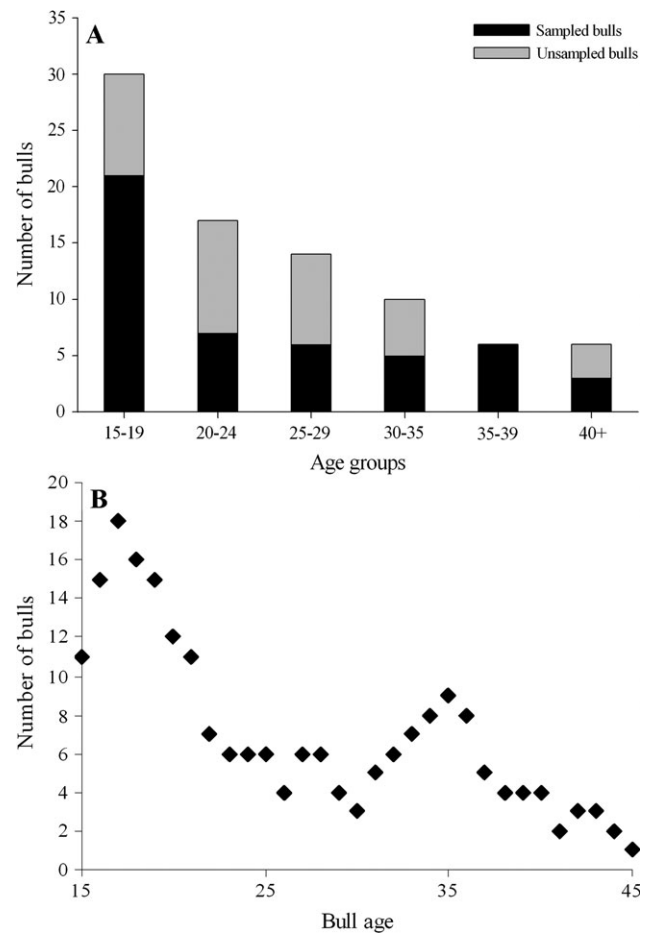


Figure 1
 (A) The age distribution and number of sampled males in the group of 83 regularly occurring males. (B) Age structure of sampled males in the Samburu population between 1996 and 2000.

end of the study period). The last parameter, proportion of sires sampled, was unknown. Decreasing the estimated proportion of fathers sampled makes the Cervus predictions more conservative but does not change the ranking between the candidates. A guideline as to whether this proportion is set correctly can be obtained by comparing the predicted fraction of calves with resolved paternities with the actual fraction resolved. Four simulations were run with values of 0.20, 0.40, 0.60, and 0.80. The simulation based on a value of 0.40 gave the best match between predicted and actual fraction of calves with resolved paternities and was therefore used.

Allele matches between assigned father, calf, and the calf's mother were used to evaluate if candidate father/calf assignments were plausible. Candidate fathers with one or nil mismatches with a calf and a higher than 95% confidence of paternity assigned by Cervus were identified and considered to be "true" fathers. In the group of calves with "true" fathers, the second most likely candidate father ($n = 25$) was identified and assumed to be, by chance, a well-matching "nonfather". The numbers of mismatches in these 25 "nonfathers" were used to delineate the threshold number of mismatches above which paternity was excluded due to incompatibilities. Only 3 of the 25 well-matching "nonfathers" had less than 3 CF/C genotype mismatches, and only 1 had less than 5 CF/C/M mismatches. Therefore, candidate fathers with greater than or equal to 3 CF/C and greater than or equal to 5 CF/C/M mismatches were excluded as fathers, regardless of likelihood and assignment test results. Finally, relatedness between all assigned fathers and mothers of the offspring (when available) was investigated using the program Relatedness 5.0 (Queller and Goodnight 1989) to ensure that paternity assignment was not caused by shared maternal heritage.

Among the 88 sampled males, no candidates less than 20 years of age were assigned paternity with more than 80% confidence. The 40 sampled males younger than 20 years at the end of the study period were therefore removed as potential candidates in order to eliminate the possibility that these bulls affected the confidence levels of other realistic candidate fathers. The paternity assignment was then rerun on the remaining 48 sampled males.

Age- and tactic-specific success

The relative age-specific paternity success (m_x) was defined as the proportion of assigned calves sired by bulls of a given age (at time of siring) divided by the total number of bulls of that age between 1996 and 2000. To account for the ± 3 -year error on bull age estimates (Rasmussen et al. 2005), m_x was calculated based on bulls and calves ± 3 years of a given age i as

$$m_x = \left(\frac{\sum_{i-3}^{i+3} c_i}{c_T} \right) / \sum_{i-3}^{i+3} m_i,$$

where c_i is the number of calves with fathers of age i , c_T is the total number of calves assigned, and m_i is the number of males of age i . The relative age- and tactic-specific contribution to reproduction was calculated for 6 age categories (15–19, 20–24, 25–29, 30–34, 35–39, 40+ years) by multiplying the average m_x within these groups with the total number of regularly observed males within each age group (using the age of bulls in 1998).

Conceptions where the assigned fathers were observed in musth (exhibiting urine dribbling) ± 2 weeks of the estimated date of conception were categorized as musth sired, whereas conceptions assigned to fathers observed but not in musth were defined as nonmusth sired. If the sire was not observed during this period, it was recorded as unknown. The tactic-

specific contribution was calculated as the proportion of calves sired by musth or nonmusth bulls per age group and multiplied by the total estimated contribution of that age group.

RESULTS

Assigned paternity

Candidate fathers were assigned to 42 calves (53%) with more than 80% confidence. All the second most likely fathers had high levels of incompatibilities and, as a result, were excluded. The most likely candidate fathers of 6 calves (all assigned under relaxed 80% confidence) were also excluded because more than 3 CF/C and/or 5 CF/C/M mismatches were found. None of the remaining most likely fathers were related to the mother of the calf. Hence, 36 of the 79 calves (46%) were considered to have resolved paternity with 31 at 95% confidence and 5 at 80% confidence. Due to the high number of loci used for assignment, very few type II errors are expected (i.e., true father among sampled males but calf assigned with less than 80% confidence). Hence, the 43 unassigned calves are assumed to have been sired by males from the group of unsampled males or by completely unknown males in adjacent lying areas.

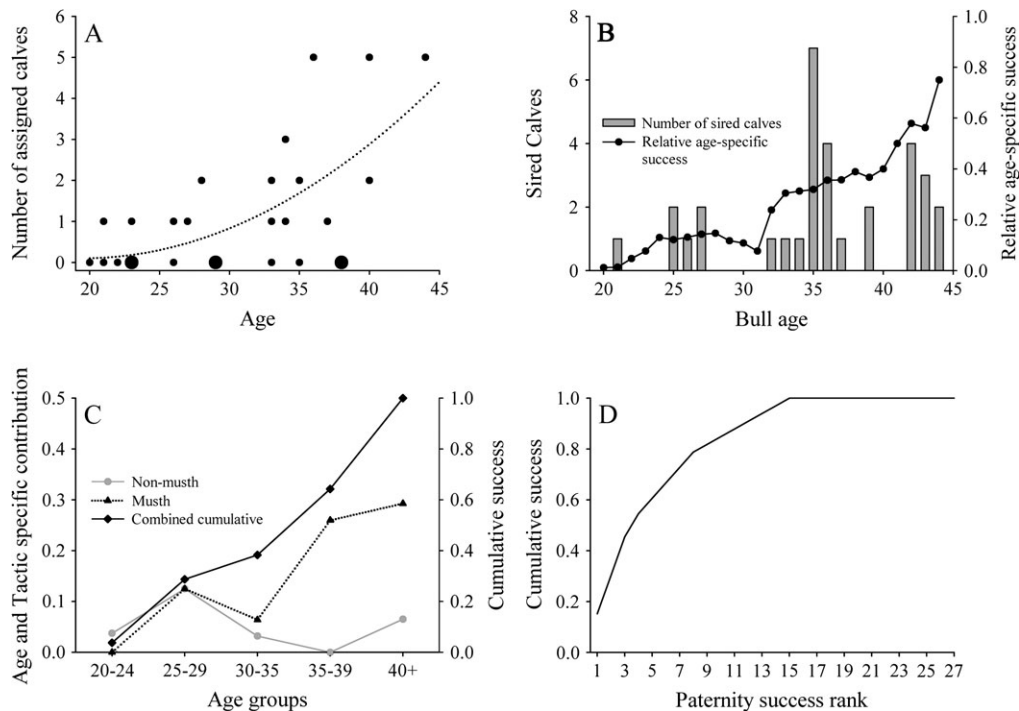
Age- and tactic-specific reproductive success

All 36 calves with resolved paternity were observed less than 2 weeks after their estimated birth date. Dates of conception were estimated by subtracting the average gestation period of 656 days (Moss 1983) from the birth date, allowing conceptions to be matched to the age and reproductive state of the fathers. In the group of calves considered to have resolved paternity, 33 (92%) were fathered by regularly occurring bulls whereas only 3 (8%) were assigned to the group of sporadically observed bulls, which mainly stay in regions adjacent to the study area. As the sporadically occurring males had limited success and the fraction of calves with resolved paternity roughly corresponded to the fraction of regular males sampled, the age- and tactic-specific paternity success was estimated using the proportion of sampled regular bulls alone.

The number of assigned calves per individual bull was positively correlated with age of bull, but age only explained half the rank variance ($r_s = 0.48$; $N = 27$; $P = 0.01$) (Figure 2A). The relative age-specific paternity success increased with age (Figure 2B) but with an apparent, short-term reduction in success occurring around the age of 30 years. After correction for the number of individuals in each age group, approximately 38% of reproduction was assigned to males less than 35 years and approximately 20–25% resulting from bulls not in musth (Figure 2C). Interestingly, a 45-year-old bull regularly seen in musth sired 2 calves outside his normal musth period. The 3 most successful bulls together sired 45% of the assigned calves (Figure 2D) corresponding to less than 20% of the genotyped calves. Based on the frequency of successful sires in each age group, it was estimated that 60% of all males older than 20 years sired at least one offspring during the 5-year study period. Although this estimate is subject to some variation due to sample size, it is likely a conservative estimate because only 25% of calves were genotyped.

DISCUSSION

The majority of calves were fathered by musth males in the oldest age groups, supporting the behavioral predictions by Poole (Poole 1989b) that musth males are the most successful sires. Males more than 50 years old were not sampled in the study population (elephants can live 60+ years in the wild);

**Figure 2**

(A) Correlation between paternity success and age of males, where a quadratic trend has been added to describe the relationship (calves = $0.0013 \times \text{age}^2 - 0.05 \times \text{age} + 0.5$; $R^2 = 0.48$). Large symbols indicate 2 data points. (B) The age-specific paternity success (m_x) (line, primary y axis) and the number of calves sired by a given aged father (bars, secondary y axis). Note the apparent reduction occurring around the age of 30 years. (C) The relative contribution of musth and nonmusth in each age group corrected for the total number of individuals in each group (primary y axis) and the combined cumulative contribution to reproduction (secondary y axis). Musth reproduction in the 25–29 years age group resulted from opportunistic musth signaling that ceased when confronted by older musth males. (D) Cumulative contribution to resolved reproduction of individual males ranked according to decreasing success.

therefore, we were unable to test if reproductive success declines with age beyond 50 years. The continuous postmaturation increase in paternity success is contrary to the general pattern seen in many mammalian species where a gradual decline generally occurs after a peak in early adulthood (Clutton-Brock 1988). This supports predictions that sexual selection has at least partially shaped the life-history traits of indeterminate growth and delayed competitive breeding in males and potentially contributed to longevity that is also favored in females (McComb et al. 2001).

The older males had the highest paternity success; however, the 3 most successful males (44, 40, and 36 years old) sired less than 20% of the genotyped calves with an estimated 60% of all males above 20 years siring offspring during the 5-year study. Because only 25% of calves in the study population were sampled, this fraction is likely a conservative estimate. Likewise, 38% of the calves with resolved paternities were sired by males less than 35 years. Hence, reproductive skew was lower than predicted from behavioral studies and less than reported in many other mammalian systems (Clutton-Brock and Isvaran 2006), including pinnipeds where a single alpha elephant seal male typically sire around 50% of the calves (Hoelzel et al. 1999) and fallow deer where the most successful male sire around 40% of the offspring (Say et al. 2003), but comparable to some polygynous systems with intermediate association between male and females (Clutton-Brock and Isvaran 2006). This lower than expected reproductive skew may be caused by reduced male monopolization of breeding opportunities due to the low frequency and unpredictable occurrence of receptive females in this species.

Reduced breeding monopolization may be exacerbated in the study populations relative to other regions as a result of the ecological characteristics of 2 wet seasons driving 2 distinct annual peaks in breeding (Rasmussen et al. 2006). As a male's musth period typically only covers one of the 2 seasons (Rasmussen 2005), this seasonal pattern may contribute to a reduction in the population-level reproductive skew. Likewise, variable ecological conditions between different breeding seasons drive large fluctuations in the number of females ovulating, which varies from 0% to more than 60% of available females per season (Rasmussen et al. 2006). This may favor alternative tactics. During seasons with peak numbers of estrous females, a single musth male cannot monopolize multiple females simultaneous in estrus (Rasmussen 2005). Furthermore, large males may not maintain musth during very poor seasons, when reproductive payoffs are low. As a result, the few receptive females during such seasons may be more easily mated by younger males. Comparison of reproductive skew in areas with different climatic patterns is needed to evaluate the degree to which environmental variability affects reproductive skew and success of alternative tactics.

Our results show that males in their early 20s, typically thought to be competitively excluded from reproducing, do successfully sire offspring. Hence, reproduction is not done exclusively by musth males. The approximately 20% reproductive contribution of nonmusth males suggests that an ART is employed by this age group. Age-dependent reproductive tactics are known from other herbivores, for example, bighorn sheep (Hogg and Forbes 1997), and nonterritorial ungulates

have been found to differ in optimal reproductive tactics with age due to differences in fighting ability and female choice (Forchhammer and Boomsma 1998). The occurrence of musth relatively late in the life of male elephants is in agreement with theoretical predictions of delayed competitive breeding (Whitehead 1994). Although the occurrence and duration of musth is positively correlated with age, the age of musth onset varies in the wild. In captive males where little or no intrasexual competition exists, musth signals, including urine dribbling, have been observed in individuals as young as 13 years (Ganswindt 2004). Likewise, in a population of African elephants in Pilansberg, South Africa, prolonged periods of musth were observed in young males (<19 years) during a period where no older males were present. After the introduction of older males to the park, musth in the younger males was behaviorally suppressed (Slotow et al. 2000). Younger musth males have also been reported to be forced out of musth by older more dominant males (Poole 1987, 1989a). This suggests that the shift between the non-musth and musth tactic is not directly linked to age but rather linked to the relative status/rank of the individual, which to a large extent is determined by the relative size/age of an individual. The shift between ARTs is expected to occur at the point of equal fitness (Gross 1996). Statistically testing for tactic-specific reproductive payoff at the age of 30–35 years, where the shift occurs between musth and nonmusth, was not possible with our dataset. However, an apparent reduction in age-specific success occurred in the study population around the age of 30 years (Figure 2B), coinciding with the first occurrence of regular musth periods (as opposed to sporadic periods often found for young males) (Rasmussen 2005). The shift in mating tactic may thus result in a temporary reduction in paternity success among male elephants, rather than occurring at a point of equal success as suggested by Gross (1996). These results are not conclusive and require further analysis on paternity success at switch points using larger datasets from multiple populations experiencing different ecological conditions. However, 2 nonmutually exclusive scenarios could explain depressed paternity success by elephants at their tactic switch point: 1) the need to learn the “tricks of the new trade” and establish the reliability of their musth signals among other males may be necessary before capitalizing on this tactic and 2) males around this age reach a size where they are considered a threat by dominant musth males and, therefore, actively excluded from associating with cows, probably resulting in a loss of breeding opportunities in comparison to the slightly younger 25-year-old males.

Paternity success must be viewed as the integrated result of multiple factors including female choice, male–male contests, and sperm competition. It is not clear to what degree female choice influences the overall success of younger subordinate males. Females have been shown to solicit guarding by older bulls (Moss 1983), suggesting that reproduction assigned to younger males is unlikely to be an outcome of female preference. It is more likely that these males succeed in situations where either no musth male is present or via sperm competition from matings occurring before or after guarding events by musth bulls. In these situations, several young males typically attempt to mate the female continuously without attempting to guard thus potentially making it difficult and costly for the female to avoid undesired matings (Rasmussen HB, personal observations).

Legal hunting for trophies or illegal poaching for ivory selectively targets older bulls (Eltringham and Malpas 1980; Hall-Martin 1980) shown here to be responsible for the majority of reproduction. Previous studies and the results presented here show that both behavioral and genetic effects

could arise from selective removal of older bulls. Such effects would include 1) an earlier onset of musth in younger bulls as they would no longer be repressed by older bulls, 2) increased harassment of females due to an absence of older guarding bulls and potential social chaos when younger bulls are not kept in line, and 3) reduced size of tusks if selection continues for generations, comparable to the effects seen in horn size of bighorn sheep (Coltman et al. 2003). The effects on reproductive skew and genetic effective population size is unclear. Effective population size could increase if a larger proportion of bulls contribute to the reproduction or decrease if the few remaining large bulls can further monopolize the breeding. Analysis of the genetic footprint in populations known to have gone through severe poaching events may help to understand how alterations in age structure affect reproductive patterns and ultimately population genetics.

FUNDING

International Elephant Foundation; Iain Douglas-Hamilton's Dawkins prize for animal welfare; Balliol College; Danish Agency for International Development (104.Dan.8.L.307, 104.Dan.8.L.316); Danish National Science Research Council (272-05-0414); National Science Foundation (IRFP OISE0502340).

We would like to thank the Office of the President, Republic of Kenya, Kenya Wildlife Service, and Samburu and Isiolo county council for permission to conduct this research.

REFERENCES

- Amos W, Twiss S, Pomeroy PP, Anderson SS. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proc R Soc Lond B Biol Sci.* 252:199–207.
- Barnes RFW. 1982. Mate searching behaviour of the elephant bulls in a semi-arid environment. *Anim Behav.* 30:1217–1223.
- Clutton-Brock TH. 1988. Reproductive success. Chicago: University of Chicago Press.
- Clutton-Brock TH. 1989. Mammalian mating systems. *Proc R Soc Lond B Biol Sci.* 236:339–372.
- Clutton-Brock TH, Harvey PH. 1978. Mammals, resources and reproductive strategies. *Nature.* 273:191–195.
- Clutton-Brock TH, Isvan K. 2006. Paternity loss in contrasting mammalian societies. *Biol Lett.* 2:513–516.
- Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-Brock TH, Pemberton JM. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol Ecol.* 8:1199–1209.
- Coltman DW, O'Donoghue P, Jorgensen TJ, Hogg JT, Strobeck C, Festa-Bianchet M. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature.* 426:655–658.
- Dakin EE, Avise JC. 2004. Microsatellite null alleles in parentage analysis. *Heredity.* 93:504–509.
- Eltringham SK, Malpas RC. 1980. The decline in elephant numbers in Rwenzori and Kabalega National Parks, Uganda. *Afr J Ecol.* 18:73–86.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science.* 197:215–223.
- Forchhammer MC, Boomsma JJ. 1998. Optimal mating strategies in nonterritorial ungulates: a general model tested on muskoxen. *Behav Ecol.* 9:136–143.
- Ganswindt A. 2004. Endocrine, physical and behavioural correlates of musth in African elephants (*Loxodonta africana*). Munster (Germany): University of Westfalen.
- Ganswindt A, Rasmussen HB, Heistermann M, Keith J. 2005. The sexually active states of free-ranging male African elephants (*Loxodonta africana*): defining musth and non-musth using endocrinology, physical signals, and behavior. *Horm Behav.* 47:83–91.
- Gemmell NJ, Burg TM, Boyd IL, Amos W. 2001. Low reproductive success in territorial male Antarctic fur seals (*Arctocephalus gazella*) suggests the existence of alternative mating strategies. *Mol Ecol.* 10:451–460.

- Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol.* 11:92–98.
- Hall-Martin AJ. 1980. Elephant survivors. *Oryx.* 15:355–362.
- Hall-Martin AJ. 1987. Role of musth in the reproductive strategy of the African elephants (*Loxodonta africana*). *S Afr J Sci.* 83: 616–620.
- Hoelzel AR, Le Boeuf BJ, Reiter J, Campagna C. 1999. Alpha-male paternity in elephant seals. *Behav Ecol Sociobiol.* 46:298–306.
- Hogg JT, Forbes SH. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. *Behav Ecol Sociobiol.* 41:33–48.
- Isvaran K. 2005. Variation in male mating behaviour within ungulate populations: patterns and processes. *Curr Sci.* 89:1192–1199.
- Jainudeen MR, Katongole CB, Short RV. 1972. Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elphas maximus*. *J Reprod Fert.* 29:99–103.
- JoGayle H, Bush M, de Vos V, Wildt DE. 1984. Electroejaculation, semen characteristics and serum testosterone concentrations of free-ranging African elephants (*Loxodonta africana*). *J Reprod Fert.* 72:187–195.
- Kahl MP, Armstrong BD. 2002. Visual displays of wild African elephants during musth. *Mammalia.* 66:159–171.
- Laws RM, Parker ISC, Johnstone RCB. 1975. Elephants and their habitat: the ecology of elephants in North Bunyoro, Uganda. Oxford: Clarendon Press.
- Lee PC, Moss CJ. 1995. Statural growth in known-age African elephants (*Loxodonta africana*). *J Zool (Lond).* 236:29–41.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol.* 7:639–655.
- Maynard-Smith J, Brown RLW. 1986. Competition and body size. *Theor Popul Biol.* 30:166–179.
- McComb K, Moss C, Drant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science.* 292:491–494.
- Moore M, Hews DK, Knapp R. 1998. Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *Am Zool.* 38:133–151.
- Morin PA, Wallis J, Moore JJ, Woodruff DS. 1994. Paternity exclusion in a community of wild chimpanzees using hypervariable simple sequence repeats. *Mol Ecol.* 3:469–478.
- Moss CJ. 1983. Oestrus behaviour and female choice in the African elephant. *Behaviour.* 86:167–196.
- Moss CJ. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J Zool (Lond).* 255: 145–156.
- Moss CJ, Poole JH. 1983. Relationships and social structure of the African elephants. In: Hinde RA, editor. *Primate social relationships: an integrated approach.* Oxford: Blackwell Scientific. p. 315–325.
- Okello J, Wittemyer G, Rasmussen HB, Douglas-Hamilton I, Nyakaana P, Arctander P, Siegmund HR. 2005. Non-invasive genotyping and Mendelian analysis of microsatellites in African Savannah elephants. *Heredity.* 96:679–687.
- Oliveira RE, Canario AVM, Grober MS. 2001. Male sexual polymorphism, alternative reproductive tactics, and androgens in comb-tooth blennies (Pisces: Blenniidae). *Horm Behav.* 40:266–275.
- Omondi P, Bitok E, Kahindi O, Mayienda R. 2002. Total aerial count of elephants in Laikipia/Samburu ecosystem. Nairobi (Kenya): Kenya Wildlife Service.
- Pemberton JM, Albon SD, Guinness FE, Clutton-Brock TH, Dover GA. 1992. Behavioural estimates of male success tested by DNA fingerprinting in a polygynous mammal. *Behav Ecol.* 3:66–75.
- Poole JH. 1987. Rutting behaviour in the African elephants: the phenomenon of musth. *Behaviour.* 102:283–316.
- Poole JH. 1989a. Announcing intent: the aggressive state of musth in African elephants. *Anim Behav.* 37:140–152.
- Poole JH. 1989b. Mate guarding, reproductive success and female choice in African elephants. *Anim Behav.* 37:842–849.
- Poole JH. 1994. Sex differences in the behaviour of African elephants. In: Short R, Balaban E, editors. *The differences between the sexes.* Cambridge: Cambridge University Press. p. 331–346.
- Poole JH, Aggeawal N, Sinange R, Nganga S, Broten M, Douglas-Hamilton I. 1992. The status of Kenya’s elephants. In: Kangwana K, editor. *AWF technical handbook, series 7.* Nairobi (Kenya): Kenya Wildlife Service and Department of Resource Surveys and Remote Sensing.
- Poole JH, Kasman LH, Ramsay EC, Lasley BL. 1984. Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*). *J Reprod Fert.* 70:255–260.
- Poole JH, Moss CJ. 1981. Musth in the African elephant, *Loxodonta africana*. *Nature.* 292:830–831.
- Poole JH, Moss CJ. 1989. Elephant mate searching: group dynamics and vocal and olfactory communication. *Symp Zool Soc (Lond).* 61: 111–125.
- Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc R Soc Lond B Biol Sci.* 270:633–640.
- Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. *Evolution.* 43:258–275.
- Rasmussen HB. 2005. Reproductive tactics in male African savannah elephants (*Loxodonta africana*). Oxford: Oxford University.
- Rasmussen HB, Wittemyer G, Douglas-Hamilton I. 2005. Estimating age of immobilized elephants from teeth impressions using dental silicon. *Afr J Ecol.* 43:215–219.
- Rasmussen HB, Wittemyer G, Douglas-Hamilton I. 2006. Predicting time specific variation in demographic processes using remote sensing data. *J Appl Ecol.* 43:366–376.
- Rasmussen LE, Buss IO, Hess DL, Schmidt MJ. 1984. Testosterone and dihydrotestosterone concentrations in elephant serum and temporal gland secretions. *Biol Reprod.* 30:352–362.
- Rubenstein DI. 1980. On the evolution of alternative mating strategies. In: Staddon JER, editor. *Limits to action.* New York: Academic Press. p. 65–100.
- Say L, Naulty F, Hayden TJ. 2003. Genetic and behavioural estimates of reproductive skew in male fallow deer. *Mol Ecol.* 12:2793–2800.
- Slotow R, van Dyk G, Poole J, Page B, Klocke A. 2000. Older bull elephants control younger males. *Nature.* 408:425–426.
- Stearns CJ. 1992. *The evolution of life histories.* Oxford: Oxford University Press.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL. 1996. Population genetics meets behavioral ecology. *Trends Ecol Evol.* 8:338–342.
- Sukumar R. 2003. *The living elephants.* Oxford: Oxford University Press.
- Uglen I, Mayer I, Rosenquist G. 2002. Variation in plasma steroids and reproductive traits in dimorphic males of corkwing wrasse (*Symphodus melops* L.). *Horm Behav.* 41:396–404.
- Whitehead H. 1994. Delayed competitive breeding in roving males. *J Theor Biol.* 166:127–133.
- Whitehouse AM, Harley EH. 2002. Paternity in the Addo elephant population, South Africa. Is a single male monopolizing matings? *Afr Zool.* 37:247–253.
- Whitehouse AM, Schoeman DS. 2003. Ranging behaviour of elephants within a small, fenced area in Addo Elephant National Park, South Africa. *Afr Zool.* 38:95–108.
- Wikelski M, Steiger SS, Gall B, Nelson KN. 2004. Sex, drug, and mating role: testosterone-induced phenotype-switching in Galapagos marine iguanas. *Behav Ecol.* 16:260–268.
- Wingfield JC. 1984. Androgens and mating systems: testosterone-induced polygony in normally monogamous birds. *Auk.* 101: 665–671.
- Wittemyer G. 2001. The elephant population of Samburu and Buffalo Springs National Reserves, Kenya. *Afr J Ecol.* 39:357–365.
- Wittemyer G, Daballen D, Rasmussen HB, Kahindi O, Douglas-Hamilton I. 2005. Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. *Afr J Ecol.* 43:44–47.
- Wright S. 1938. Size of population and breeding structure in relation to evolution. *Science.* 87:430–431.