



Adolescence in male African elephants, *Loxodonta africana*, and the importance of sociality

KATE E. EVANS & STEPHEN HARRIS

School of Biological Sciences, University of Bristol

(Received 10 December 2007; initial acceptance 17 January 2008;
final acceptance 18 March 2008; published online 24 June 2008; MS. number: 07-20014R)

The degree of sociality during an animal's life changes as it modulates its behaviour to reflect different life stages. Only a few species of mammal undergo a period of adolescence, but for these species it is probably one of their most important life stages. It is when individuals acquire skills and develop relationships that are of both immediate and long-term benefit to their survival and reproductive success, particularly in polygynous males in which sexual selection favours size and dominance. We collected focal and observational data on male African elephants in the Okavango Delta, Botswana, to assess behaviour and social interactions during adolescence. Adolescent males (10–15 and 16–20 years of age) were the most sociable age group, showing preferences for larger social groupings and being in closer proximity to other elephants; later adolescent males (ages 16–20) showed a tendency for higher social levels. Males of all ages preferred to have males ≥ 36 years of age as their nearest neighbour. We argue that this proximity to older males provides opportunities for males to learn from more experienced individuals. It has long been recognized that matriarchs are the repositories of social and ecological knowledge within elephant breeding herds: we suggest that mature males are reservoirs for such knowledge within bull society.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.

Keywords: adolescence; African elephant; dominance; hierarchy; *Loxodonta africana*; male behaviour; social learning

The life of a mammal can be broken down into four key life stages—infancy, juvenescence, adolescence and adulthood—which are characterized by both physical and behavioural differences. Juvenescence is the period between weaning and the onset of puberty (Bogin 1999). However, in many mammals the onset of puberty does not necessarily mean that they are adults and able to reproduce, and so the term adolescence is used to describe the interval between puberty and effective reproduction (Pereira & Altmann 1985). For males this transition is not complete until they are socially as well as physically capable of reproduction (Walters 1987). Characteristics of adolescence include a growth spurt, development of secondary sexual characteristics and attainment of sexual maturation. As hormonal and physical maturation proceeds, behavioural differences become apparent as individuals continue to make the transition from maternal association to integration into the adult community or

dispersal (Pereira & Altmann 1985; Pusey 1990; Setchell 2003).

In most polygynous species males are the predominant dispersers and larger sex (Greenwood 1980; Dobson 1982; Bernstein et al. 1993; Loe et al. 2006). Competition in polygynous species places a premium on characteristics that assist males in locating and mating with receptive females, and lifetime reproductive success is closely related to body size and the development of weaponry (Le Boeuf 1974; Clutton-Brock et al. 1982; Lincoln 1994; Poole 1994; Watson 1998; Connor et al. 2000; Whitehead & Weiglart 2000). It has been postulated that the prereproductive but sexually mature adolescent period in many primates may enable males to learn about their physical and social environments prior to attempting to reproduce (Poirier & Smith 1974; Bogin 1999). It also increases opportunities to learn a variety of skills and may enable a longer period of brain growth, so that the association areas of the cerebral cortex can mature (Savin-Williams & Weisfeld 1989). Thus, this learning process may benefit adult reproductive success and hence justify delaying reproduction (Walters 1987). However, there are costs, as individuals divert the

Correspondence: K. E. Evans, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K. (email: kate.evans@bristol.ac.uk).

calories that would ordinarily be used for quick growth to learning purposes.

Male African elephants have one of the longest delays in reproduction; although puberty in male elephants occurs between the ages of 9 and 15 (Short et al. 1967; Hanks & McIntosh 1973; Lee 1986), and sexual maturity is reached at 17 (Laws 1969; Poole 1994), males rarely mate until they are in their 30s (Poole 1994), with larger, older bulls getting most of the mating opportunities (Poole 1987, 1994). Mating success increases after males have experienced their first period of musth at around 29 years. Musth is a period of sexual activity in male elephants, signified by high testosterone levels, urine dribbling, green penis syndrome and swollen temporal glands (Poole & Moss 1981).

Adolescence in male elephants is generally accepted to be between the ages of 10 and 20, when puberty and sexual maturity occur and young males go through the process of independence from their natal herd. There is also a fluid hierarchal social system in elephants, which means that the early assessment of conspecifics is important, especially where encounters are unpredictable and prior knowledge of opponents could avoid costly fighting (Moss & Poole 1983). Social knowledge acquired through interactions while in their herd, in particular sparring with non-herd members, will help adolescent male elephants integrate into bull society. Young male elephants go through a second distinct phase of socialization in these all-male groups; this period is coincident with a second major stage in brain reorganization seen in humans (Bradshaw et al. 2005). However, although adolescence is an important developmental stage that constitutes a significant proportion of a male's reproductive life span in sexually dimorphic species such as elephants (Bernstein et al. 1993; Whitehead & Weilgart 2000; Setchell & Dixson 2002), few studies have examined the pattern of adolescent development. We used data collected on known elephants over a 3-year period to assess the importance of social interactions in the continued development of sexually dimorphic polygynous males and the purpose of a protracted adolescent period. In particular we examined (1) whether adolescent male elephants have higher rates of social interactions, (2) whether they associate more with same-age peers and (3) whether they prefer to be closer to same-age peers.

METHODS

Study Area

We collected data from a population of free-ranging African elephants from February 2002 to February 2005 in Wildlife Management Area NG26, in the western part of the Okavango Delta, Botswana, a traditional 'bull area' (Laws et al. 1975; Moss & Poole 1983; Moss 1988). The study area covered 215 km² centred on the research camp at S19.40420°, E22.56162° (digital degrees and minutes). It flooded annually and there were three seasons: the rainy season (November–March), the flood season (April–September) and the dry season (October). The highest elephant density occurred in the dry season,

with an estimated population of 1576 elephants within the study area; of these 333 males were individually recognized (Evans 2006). There were five main habitat types: open grassland/floodplain, mopane (*Colophospermum mopane*) woodland, mixed woodland (*Acacia* spp., *Combretum* spp.), Terminalia (*Terminalia sericea*) woodland and island vegetation (dominant plants were mainly *Hyphaene petersiana* or *Phoenix reclinata*).

Age Calculation Techniques

We classified male elephants into five age groups—10–15 years (early adolescence), 16–20 years (later adolescence), 21–25 years, 26–35 years and ≥ 36 years—using footprint measurements (Western et al. 1983; Lee & Moss 1995) to calculate shoulder height (Douglas-Hamilton 1972; Croze 1974; Douglas-Hamilton et al. 1981; Lark 1984; Jachmann 1991; Lee & Moss 1995) and a combination of visual clues such as length of tusks (Hanks 1972), tusk girth and head shape (Poole 1982).

Focal Sampling

We collected data on associations and social behaviours during 30-min sample observations undertaken throughout the study area on male elephants sighted while driving set routes. Once we located an elephant(s), we assessed its identity and age from a distance using binoculars and, if more than one male was present, we selected a focal animal by choosing an individual we had not knowingly sampled previously. We then moved the vehicle into a position from which we could observe the focal and other animals through binoculars from a minimum distance of around 50 m, exact distance from the focal animal varied with habitat and degree of visibility. We changed the position of the vehicle during the focal period only if one or more elephants moved out of view or into a position in which they were difficult to observe. On the very few occasions on which an elephant was disturbed by the presence of the vehicle (e.g. a musth male), we abandoned the observation period; we did not collect data from elephant groups that were disturbed by the presence of the vehicle.

We recorded the focal individual's social grouping (alone, with one to five other males, with more than five other males, with a female herd or with a mixed herd) and, where applicable, the identity of other individuals present, at the start of the focal period. We recorded the activity of the focal individual and the identification of, and distance to, the nearest neighbour (m) of the focal individual every 5 min. We also recorded the length and rate of any audible vocalizations. Wherever possible, we identified callers by audible (e.g. direction and intensity) and visual clues such as ear flapping, opening of the mouth (McComb 1996), listening and forehead vibrations (Poole et al. 1988). For analysis, we quantified activities as the rate per 30 min; and we averaged nearest-neighbour distance across the 30 min period.

Later we verified the identification of the focal individual at camp using digital photographs and identification files. To avoid pseudoreplication, in which repeat data had been

collected from the same individual or more than one elephant had been sampled within that social grouping, we selected at random a single focal period for analysis. Overall, we collected 283 independent focal samples from known individuals, of which 222 were of elephants in a social situation.

Statistical Analyses

Social behaviours

As the data were not normally distributed and could not be transformed, we analysed the effects of season and age on the frequency of social behaviours, greeting, sparring/playing, vocalization and distance to nearest neighbour separately using nonparametric statistics. As the dry season lasted only one month each year, the data collected during this period were limited (Table 1). Consequently, we compared only data from the rainy and flood seasons using a Mann–Whitney *U* test. We compared differences between age classes using a series of Kruskal–Wallis tests; we then identified statistically different groups using the post hoc procedures outlined by Siegel & Castellan (1988), whereby groups were compared against each other for differences using the equation

$$|\bar{R}_u - \bar{R}_v| \geq Z_{\alpha/k(k-1)} \sqrt{\frac{N(N+1)}{12} \left(\frac{1}{n_u} + \frac{1}{n_v} \right)}$$

with the critical value for *Z* being taken from the supplied table. We included all the focal data, not just social focals, in the vocalization analyses (Table 1).

Table 1. Summary of the data collected by season

Data set	Age class (years)	Rainy	Flood	Dry	Total
Total sightings of male elephants		1484	2288	300	4072
Total sightings of male groups		661	1014	99	1774
Total sightings of male elephants in male-only groups	10–15	96	171	27	294
	16–20	148	327	34	509
	21–25	179	287	27	493
	26–35	301	543	48	892
	≥36	389	480	23	892
<i>Subtotal</i>		1113	1808	159	3080
Social focal data	10–15	19	28	3	50
	16–20	21	19	2	42
	21–25	15	27	0	42
	26–35	13	26	4	43
	≥36	20	24	1	45
<i>Subtotal</i>		88	124	10	222
Focal data	10–15	19	30	3	52
	16–20	21	22	2	45
	21–25	20	30	1	51
	26–35	24	48	4	76
	≥36	26	32	1	59
<i>Subtotal</i>		110	162	11	283

Data from total sightings were used to analyse the patterns of social grouping; social focal data were used to analyse the patterns of social behaviour within groups and nearest-neighbour distances; focal data were used to analyse the patterns of activity and vocalization.

Social groupings

We quantified patterns of association of individual male elephants in different age classes using all observations (i.e. focal and nonfocal) of animals seen during the study. Each time we observed a male elephant, we recorded the number of male and female elephants within 500 m. Assuming that the presence of more than one animal together represents a ‘choice’ of all individuals to associate with one another, we recorded data separately for every animal in each social grouping observed, i.e. we would categorize every animal in the cluster as having been in that group of individuals. We analysed differences in the mean observed group size between age classes using a Kruskal–Wallis test. In case any observed differences in mean group size between age classes were an artefact of associations with females, we also analysed the data considering only sightings of all-male groupings.

We examined patterns of association between males of different age classes using simple association indices (Ginsberg & Young 1992). We calculated the association index between two particular age classes as $R = X / (N - D)$, where *X* is the number of viewing periods in which animals of age class A and age class B were seen together, *N* is the total number of viewing periods across all age classes and *D* is the number of viewing periods in which animals of neither age class A nor age class B were sighted. We analysed the frequencies with which animals of a given age class were sighted with males in each age class using chi-square tests, assuming an expected equal distribution.

We analysed preferences for nearest neighbour using chi-square tests on the data from male-only groups. First we carried out a test to see if the choice of nearest neighbour was nonrandom. If that was the case, we then removed the highest partial value and recalculated χ^2 . We repeated this until χ^2 was nonsignificant.

RESULTS

Social Behaviours

The distribution of focal samples by age class and season is summarized in Table 1. Season did not affect the total frequency of social behaviours per half-hour focal (Mann–Whitney test: $W_{88,124} = 9800, P = 0.145$) or sparring/playing ($W_{88,124} = 9349, P = 0.908$) by focal individuals. However, it did affect the rate of greeting ($W_{88,124} = 9863, P = 0.046$), which was more common during the rainy season. The frequency of social behaviours (Fig. 1) did not vary significantly with age (Kruskal–Wallis test: $H_4 = 9.11, P = 0.058$) nor did sparring/playing ($H_4 = 1.82, P = 0.769$). However, the rate of greeting varied significantly with age ($H_4 = 13.31, P = 0.010$), with males 16–20 years of age showing the highest greeting rates. Post hoc testing procedures showed that the rate of greeting was lowest in males ≥36 years of age (Fig. 1). Conversely, age did not affect the frequency at which focal males were greeted by other individuals ($H_4 = 3.38, P = 0.496$).

The rate of vocalization per half-hour focal was not affected by season ($W_{110,162} = 14\,540, P = 0.144$) or age

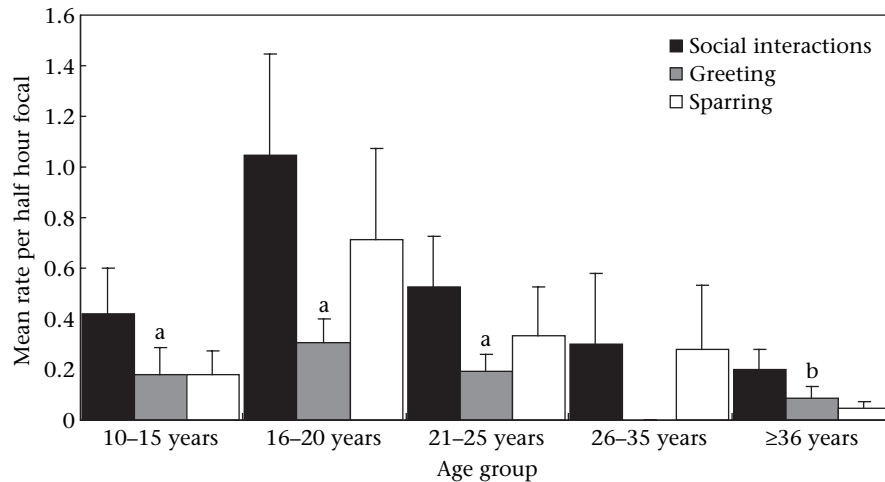


Figure 1. Mean (+SE) rate of social interactions, greeting and sparring per half-hour focal by age group; for social focal sample sizes see Table 1. Letters above the bars denote significantly different groups as identified by post hoc comparisons.

($H_4 = 8.83$, $P = 0.066$), although there was a tendency for males ≥ 36 years of age to vocalize audibly more often; we excluded focal data collected from musth males, as this significantly affects their tendency to vocalize (Poole 1987).

Social Groupings

Age significantly affected the number of male and female elephants with which individual males were sighted (Kruskal–Wallis test: $H_4 = 431.53$, $P < 0.001$; $N = 4072$ sightings of male elephants). Mean group size declined significantly with increasing age class, with the exception of males 26–35 and ≥ 36 years of age, which were not significantly different (Fig. 2).

All-male groupings ($N = 1774$) varied in size from 1 to 17 individuals, with a mean of 2, median of 1 and a mode of 1. The size of all-male groupings was affected by season ($H_2 = 15.88$, $P < 0.001$) and age ($H_4 = 51.00$,

$P < 0.001$), with younger males being sighted in larger groups (Fig. 2). However, males of all age classes did not associate equally with males of other age classes (10–15 years: $\chi_4^2 = 119.63$, $P < 0.001$; 16–20 years: $\chi_4^2 = 99.81$, $P < 0.001$; 21–25 years: $\chi_4^2 = 10.26$, $P = 0.036$; 26–35 years: $\chi_4^2 = 30.53$, $P < 0.001$; ≥ 36 years: $\chi_4^2 = 15.09$, $P = 0.004$); all age groups spent a higher proportion of time in groups with males of a similar age (Fig. 3). Because larger groups of males potentially allow greater flexibility in the choice of nearest neighbours, we repeated the analysis using only groups of three or more males. However, all age groups still preferred to be closest to males ≥ 36 years of age (10–15 years: $\chi_4^2 = 14.12$, $P = 0.007$; 16–20 years: $\chi_4^2 = 47.93$, $P < 0.001$; 21–25 years: $\chi_4^2 = 123.92$, $P < 0.001$; 26–35 years: $\chi_4^2 = 100.77$, $P < 0.001$; ≥ 36 years: $\chi_4^2 = 78.26$, $P < 0.001$).

Season did not affect the distance to nearest neighbour (Kruskal–Wallis test: $H_2 = 3.82$, $P = 0.148$), but age did ($H_4 = 17.68$, $P = 0.001$), with median distance increasing

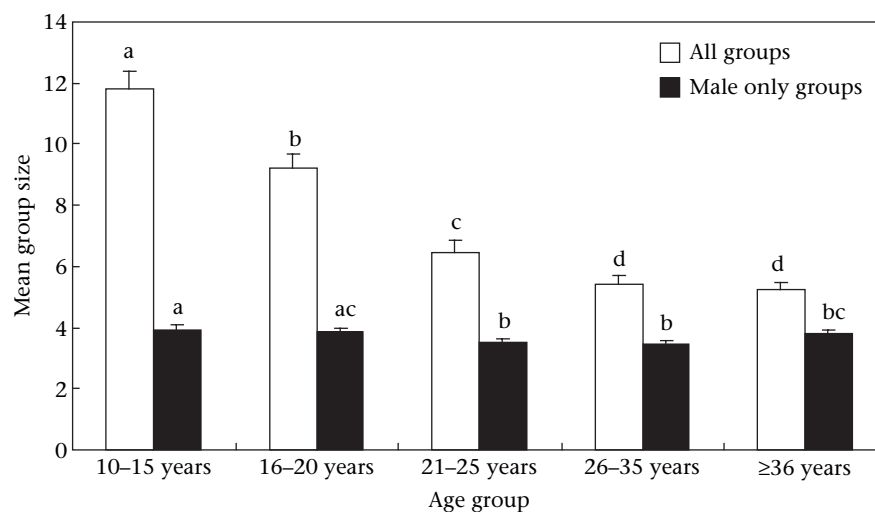


Figure 2. Mean (+SE) group size of males of different age classes sighted in male and female groups and male-only groups; for focal sample sizes see Table 1. Letters above the bars denote significantly different groups as identified by post hoc comparisons.

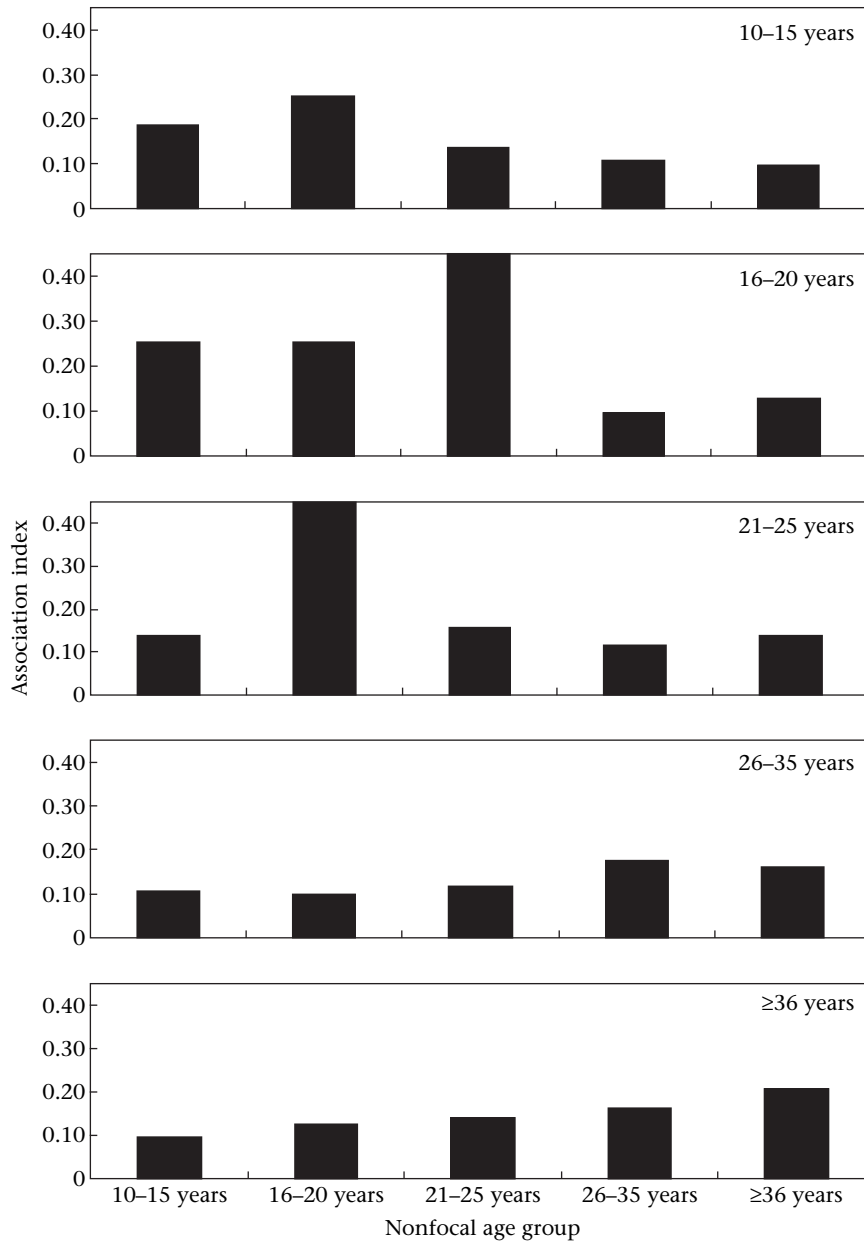


Figure 3. Association indexes of males within different age classes; for social focal sample sizes see Table 1. The age group of the focal age class is on the right-hand side.

with increasing age (Fig. 4). Male elephants preferred to be closer to older elephants (Table 2); males 10–15 years of age were least likely to be closest to other males 10–15 years of age ($\chi^2_4 = 70.94$, $P < 0.001$) and males of all age groups preferred to be closest to males ≥ 36 years of age (10–15 years: $\chi^2_3 = 8.65$, $P = 0.03$; 16–20 years: $\chi^2_4 = 70.94$, $P < 0.001$; 21–25 years: $\chi^2_4 = 122.46$, $P < 0.001$; 26–35 years: $\chi^2_4 = 146.98$, $P < 0.001$; ≥ 36 years: $\chi^2_4 = 317.83$, $P < 0.001$; Fig. 5).

DISCUSSION

Adolescence in male African elephants is an important social period, reflected in higher levels of social interactions

and a preference for being in larger social groups than older males. It is an intense period of learning and development as adolescent males interact with new elephants and explore new areas, while also establishing themselves in the dominance hierarchy. They can gather information about new areas and learn about the new social system they have entered, using the mature bulls as social and ecological repositories of knowledge. Therefore postprime bulls still have an important part to play in the social system of male elephants.

Sparring occurs most often between males of a similar age, and thus comparable skill, to establish and reinforce the hierarchy that dominates such male societies (Miller & Byers 1998). Season affects the rate of social interactions

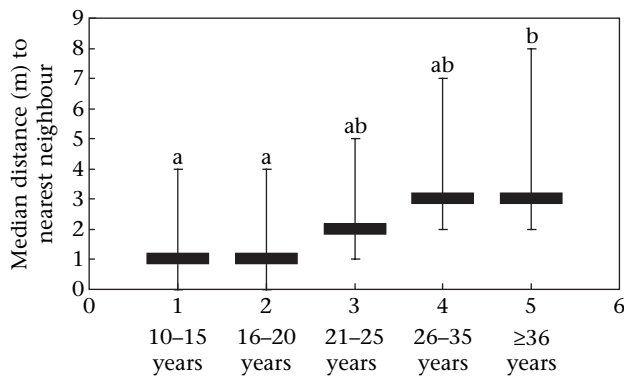


Figure 4. Median (\pm interquartile range) distance (m) between focal males and their nearest neighbour during half-hour focal observations; for focal sample sizes see Table 1. Letters above the bars denote significantly different groups as identified by post hoc comparisons.

in many mammals (Sommer & Mendoza-Granados 1995) and, whereas greeting in male elephants was affected by season, sparring was not, highlighting the importance of this activity and the importance for male elephants of asserting their dominance at every opportunity. Sexual selection often favours large body size in sexually dimorphic polygynous species (Alexander et al. 1979; Clutton-Brock et al. 1982; Poole 1987; Haley et al. 1994). Therefore, by establishing themselves in the hierarchy when adolescent, males can devote more time to feeding, thereby increasing the rate of growth and avoiding dangerous conflict, reaping the rewards when they are mature (Poirier & Smith 1974; Hall 1998). Sparring rate declined with age, which is indicative of the establishment of a social hierarchy and the ritualism of male–male competition. It is rare that size is the only predictor of mating success; male rank and/or fighting ability are other indicators (Clutton-Brock et al. 1982; Moore et al. 1995; Constable et al. 2001; Say et al. 2001). This is especially so when mate guarding is the principal means by which males gain access to sexually receptive females, e.g. elephant seals, *Mirounga angustirostris* (Haley et al. 1994); Soay sheep, *Ovis aries* (Preston et al. 2001) and African elephants (Poole 1989a).

The higher rate of greeting among younger males and the elevated rates of sparring in later adolescence occurred during the period when males meet new peers and assert themselves in the hierarchy. Adolescent male elephants

Table 2. Number of observations of focal individuals with their nearest neighbour by age groups

Age group of focal individual (years)	Age group of nearest neighbour (years)				
	10–15	16–20	21–25	26–35	≥36
10–15	12	31	33	36	54
16–20	26	63	57	19	94
21–25	13	57	41	86	130
26–35	3	24	51	101	106
≥36	31	50	81	90	257

used an area of 1721–10 168 km² (mean 4824 km², unpublished data) in the Okavango Delta. If adult males use a comparative size, it is likely that they will continually meet new and old acquaintances and so sparring remains important to establish and maintain positions in the hierarchy.

Adolescent males (10–20 years of age) were the most social age class; we recorded them in the largest groups and they had the lowest nearest-neighbour distances. Associating with similarly aged males will enable an individual to establish his position in the hierarchy (Poole 1989b). In particular, greeting and sparring with peers within their own and other herds, and greeting males generally, play a role in the establishment of social position and familiarization with social etiquette for young males. Opportunities for males to learn from older individuals may come through males being closer to older bulls, as is thought to be the case with pronghorns, *Antilocapra americana* (Miller & Byers 1998), chimpanzees, *Pan troglodytes* (Pusey 1990) and savannah baboons, *Papio cynocephalus* (Pereira 1988).

However, this pattern of association was not limited to adolescents, as males of all age classes preferred males ≥ 36 years as their nearest neighbour. It has long been recognized that young elephants learn from females within the herd (Lee & Moss 1986, 1999), and observations from captive elephants indicate that they are quick to learn from older individuals (de Alwis 1991; Daim 1995; McKnight 1995; Lee & Moss 1999). In females, this extends beyond sexual maturity, with matriarchs passing on knowledge of the local area (Viljoen 1989; McComb et al. 2001) and older females assisting in the birth and raising of calves (Moss 1988). At independence male elephants change their social environment, from the highly structured breeding herd to the much more fluid social system of adult males, in which they must learn to traverse and forage within new areas as well as learning the rules of bull society. Joining up with conspecifics and proximity to experienced individuals may facilitate these physically independent but naïve individuals to deal with their new social and physical environment (Pereira & Altmann 1985; Stamps 1987; Box 1999). In particular, socializing with older conspecifics will enable dispersing males to learn the locations of profitable foraging areas (Stamps 1987). This enables them to reduce the time they expend gathering information so that more time can be devoted to growth and socializing.

The significance of older males in regulating the behaviour of younger individuals has been shown in recent repopulation and translocation programs in South Africa. Here, in the absence of older bulls, young males caused a number of management problems through inappropriate behaviour (Slotow & van Dyk 2001; Slotow et al. 2001). These problems are thought to arise because the young males come into musth prematurely (Slotow et al. 2000), which is normally suppressed by older bulls (Rasmussen & Krishnamurthy 2000; Slotow et al. 2000). Other factors involved in these abnormal behaviours include attachment disruptions and relational trauma (Bradshaw & Schore 2007). It is possible therefore that older males may be the ones choosing to be closer to the

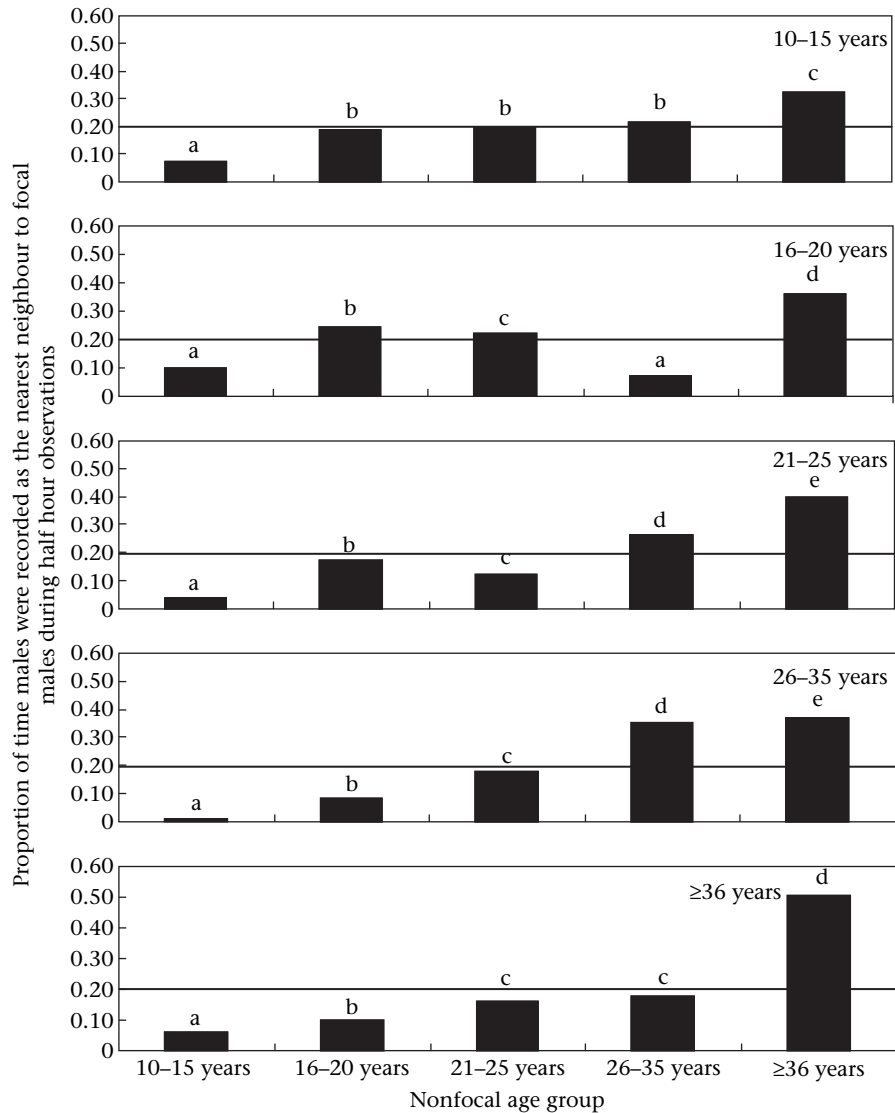


Figure 5. Percentage of time males in different age categories were recorded as the nearest neighbour to focal males during half-hour observations; for focal sample sizes see Table 2. The age group of the focal age class is on the right-hand side. Letters above the bars denote significantly different groups as identified by post hoc comparisons. Horizontal lines denote expected values.

younger males, to suppress musth and eliminate mating competition. In addition, we cannot rule out the possibility of kin recognition and that old bulls are providing protection to related males (Petrie et al. 1999).

The behavioural characteristics of adolescence seen in many mammals, such as increased risk taking (Berndt 1979; Galef 1981; Compas et al. 1995; Madu & Matla 2003), an increase in playful and affiliate behaviour (Bernstein et al. 1993; Laviola & Adriani 1998) and their strong inner drive to explore (Poirier & Smith 1974; Galef 1981), facilitate independence. Once independent, the higher levels of social interaction in adolescent male elephants and their preference for being in larger social groupings, closer to other elephants and, in particular, closer to older elephants suggest that adolescent male elephants are gaining information from conspecifics.

It has long been accepted that matriarchs are the repositories of knowledge within female elephant social

systems (Moss 1988; McComb et al. 2001). Our work suggests that adolescence in male African elephants is an important learning period, enabling them to gain information from older bulls that will assist them to become dominant males without posing a competitive threat. Thus mature males are important in the stability of bull society, playing a role comparable to that of the matriarchs in the breeding herds.

Acknowledgments

We thank Elephant Back Safaris (P) Ltd, The Whitley Wildlife Conservation Fund and the Dulverton Trust for funding; the Office of the President, the Ministry of Environment, Wildlife and Tourism and the Department of Wildlife and National Parks for permission to work in Botswana; and the Harry Oppenheimer Okavango Research Centre for their support.

References

- Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M. & Sherman, P. W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. In: *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective* (Ed. by N. A. Chagnon & W. Irons), pp. 402–435. Boston, Massachusetts: Duxbury Press.
- de Alwis, L. 1991. Working elephants. In: *The Illustrated Encyclopedia of Elephants: from Their Origins and Evolution to Their Ceremonial and Working Relationship with Man* (Ed. by S. K. Eltringham & D. Ward), pp. 116–129. New York: Crescent Books.
- Berndt, T. J. 1979. Developmental changes in conformity to peers and parents. *Developmental Psychology*, **15**, 608–616.
- Bernstein, I. S., Judge, P. G. & Ruehlmann, T. E. 1993. Sex differences in adolescent rhesus monkey (*Macaca mulatta*) behavior. *American Journal of Primatology*, **31**, 197–210.
- Bogin, B. 1999. Evolutionary perspective on human growth. *Annual Review of Anthropology*, **28**, 109–153.
- Box, H. O. 1999. Temperament and socially mediated learning among primates. *Symposia of the Zoological Society of London*, **72**, 33–56.
- Bradshaw, G. A. & Schore, A. N. 2007. How elephants are opening doors: developmental neuroethology, attachment and social context. *Ethology*, **113**, 426–436.
- Bradshaw, G. A., Schore, A. N., Brown, J. L., Poole, J. H. & Moss, C. J. 2005. Elephant breakdown. Social trauma: early disruption of attachment can affect the physiology, behaviour and culture of animals and humans over generations. *Nature*, **433**, 807.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer: Behavior and Ecology of the Two Sexes*. Edinburgh: Edinburgh University Press.
- Compas, B. E., Hinden, B. R. & Gerhardt, C. A. 1995. Adolescent development: pathways and processes of risk and resilience. *Annual Review of Psychology*, **46**, 265–293.
- Connor, R. C., Read, A. J. & Wrangham, R. 2000. Male reproductive strategies and social bonds. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 247–269. Chicago: University of Chicago Press.
- Constable, J. L., Ashley, M. V., Goodall, J. & Pusey, A. E. 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology*, **10**, 1279–1300.
- Croze, H. 1974. The Seronera bull problem. I. The elephants. *East African Wildlife Journal*, **12**, 1–27.
- Daim, M. S. 1995. Elephant translocation: the Malaysian approach. In: *A Week with Elephants: Proceedings of the International Seminar on Asian Elephants* (Ed. by J. C. Daniel & H. Datye), pp. 242–248. Oxford: Oxford University Press.
- Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30**, 1183–1192.
- Douglas-Hamilton, I. 1972. On the ecology and behaviour of the African elephant: elephants of Lake Manyara. D.Phil. thesis, Oxford University.
- Douglas-Hamilton, I., Hillman, A. K. K. & Moss, C. J. 1981. Notes on the vertical photography of elephants for age determination. *ILCA Monographs*, **4**, 131–142.
- Evans, K. E. 2006. The behavioural ecology and movements of adolescent male African elephant (*Loxodonta africana*) in the Okavango Delta, Botswana. Ph.D. thesis, Bristol University.
- Galef, B. G. 1981. The ecology of weaning: parasitism and the achievement of independence by altricial mammals. In: *Parental Care in Mammals* (Ed. by D. J. Gubernick & P. H. Klopfer), pp. 211–241. New York: Plenum.
- Ginsberg, J. R. & Young, T. P. 1992. Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, **44**, 377–379.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Haley, M. P., Deutsch, C. J. & Le Boeuf, B. J. 1994. Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behaviour*, **48**, 1249–1260.
- Hall, S. L. 1998. Object play by adult animals. In: *Animal Play—Evolutionary, Comparative, and Ecological Perspectives* (Ed. by M. Bekoff & J. A. Byers), pp. 45–60. Cambridge: Cambridge University Press.
- Hanks, J. 1972. Growth of the African elephant (*Loxodonta africana*). *East African Wildlife Journal*, **10**, 251–272.
- Hanks, J. & McIntosh, J. E. A. 1973. Population dynamics of the African elephant (*Loxodonta africana*). *Journal of Zoology*, **169**, 29–38.
- Jachmann, H. 1991. Evaluation of four survey methods for estimating elephant densities. *African Journal of Ecology*, **29**, 188–195.
- Lark, R. M. 1984. A comparison between techniques for estimating the ages of African elephants (*Loxodonta africana*). *African Journal of Ecology*, **22**, 69–71.
- Laviola, G. & Adriani, W. 1998. Evaluation of unconditioned novelty-seeking and *d*-amphetamine-conditioned motivation in mice. *Pharmacology Biochemistry and Behavior*, **59**, 1011–1020.
- Laws, R. M. 1969. Aspects of reproduction in the African elephant, *Loxodonta africana*. *Journal of Reproduction and Fertility Supplement*, **6**, 193–217.
- Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. 1975. *Elephants and Their Habitats: the Ecology of Elephants in North Bunyoro, Uganda*. Oxford: Clarendon Press.
- Le Boeuf, B. J. 1974. Male–male competition and reproductive success in elephant seals. *American Zoologist*, **14**, 163–176.
- Lee, P. C. 1986. Early social development among African elephant calves. *National Geographic Research*, **2**, 388–401.
- Lee, P. C. & Moss, C. J. 1986. Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology*, **18**, 353–361.
- Lee, P. C. & Moss, C. J. 1995. Statural growth in known-age African elephants (*Loxodonta africana*). *Journal of Zoology*, **236**, 29–41.
- Lee, P. C. & Moss, C. J. 1999. The social context for learning and behavioural development among wild African elephants. *Symposia of the Zoological Society of London*, **72**, 102–125.
- Lincoln, G. A. 1994. Teeth, horns and antlers: the weapons of sex. In: *The Differences between the Sexes* (Ed. by R. V. Short & E. Balaban), pp. 131–158. Cambridge: Cambridge University Press.
- Loe, L. E., Irvine, R. J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S. D., Mysterud, A. & Stenseth, N. C. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology*, **75**, 485–496.
- Madu, S. N. & Matla, M. P. 2003. Illicit drug use, cigarette smoking and alcohol drinking behaviour among a sample of high school adolescents in the Pietersburg area of the Northern Province, South Africa. *Journal of Adolescence*, **26**, 121–136.
- McComb, K. 1996. Studying vocal communication in elephants. In: *Studying Elephants* (Ed. by K. Kangwana), pp. 112–119. Nairobi: African Wildlife Foundation.
- McComb, K., Moss, C., Durant, S. M., Baker, L. & Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science*, **292**, 491–494.
- McKnight, B. 1995. Behavioural ecology of ‘hand-reared’ African elephants (*Loxodonta africana* (Blumenbach)) in Tsavo East National Park, Kenya. *African Journal of Ecology*, **33**, 242–256.

- Miller, M. N. & Byers, J. A. 1998. Sparring as play in young pronghorn males. In: *Animal Play: Evolutionary, Comparative, and Ecological Perspectives* (Ed. by M. Bekoff & J. A. Byers), pp. 141–160. Cambridge: Cambridge University Press.
- Moore, N. P., Kelly, P. F., Cahill, J. P. & Hayden, T. J. 1995. Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behavioral Ecology and Sociobiology*, **36**, 91–100.
- Moss, C. 1988. *Elephant Memories: Thirteen Years in the Life of an Elephant Family*. London: Elm Tree Books.
- Moss, C. J. & Poole, J. H. 1983. Relationships and social structure of African elephants. In: *Primate Social Relationships: an Integrated Approach* (Ed. by R. A. Hinde), pp. 315–325. Oxford: Blackwell Scientific.
- Pereira, M. E. 1988. Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*. *Animal Behaviour*, **36**, 184–204.
- Pereira, M. E. & Altmann, J. 1985. Development of social behavior in free-living nonhuman primates. In: *Nonhuman Primate Models for Human Growth and Development* (Ed. by E. S. Watts), pp. 217–309. New York: A. R. Liss.
- Petrie, M., Krupa, A. & Burke, T. 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature*, **401**, 155–157.
- Poirier, F. E. & Smith, E. O. 1974. Socializing functions of primate play. *American Zoologist*, **14**, 275–287.
- Poole, J. H. 1982. Musth and male–male competition in the African elephant. Ph.D. thesis, Cambridge University.
- Poole, J. H. 1987. Rutting behaviour in African elephants: the phenomenon of musth. *Behaviour*, **102**, 283–316.
- Poole, J. H. 1989a. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour*, **37**, 842–849.
- Poole, J. H. 1989b. Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour*, **37**, 140–152.
- Poole, J. H. 1994. Sex differences in the behaviour of African elephants. In: *The Differences between the Sexes* (Ed. by R. V. Short & E. Balaban), pp. 331–346. Cambridge: Cambridge University Press.
- Poole, J. & Moss, C. 1981. Musth in the African elephant, *Loxodonta africana*. *Nature*, **292**, 830–831.
- Poole, J. H., Payne, K., Langbauer, W. R. & Moss, C. J. 1988. The social contexts of some very low frequency calls of African elephants. *Behavioral Ecology and Sociobiology*, **22**, 385–392.
- Preston, B. T., Stevenson, I. R., Pemberton, J. M. & Wilson, K. 2001. Dominant rams lose out by sperm depletion. *Nature*, **409**, 681–682.
- Pusey, A. E. 1990. Behavioural changes at adolescence in chimpanzees. *Behaviour*, **115**, 203–246.
- Rasmussen, L. E. L. & Krishnamurthy, V. 2000. How chemical signals integrate Asian elephant society: the known and the unknown. *Zoo Biology*, **19**, 405–423.
- Savin-Williams, R. C. & Weisfeld, G. E. 1989. An ethological perspective on adolescence. In: *Biology of Adolescent Behavior and Development* (Ed. by G. R. Adams, R. Montemayor & T. P. Gullotta), pp. 249–274. London: Sage.
- Say, L., Pontier, D. & Natoli, E. 2001. Influence of oestrus synchronization on male reproductive success in the domestic cat (*Felis catus* L.). *Proceedings of the Royal Society of London, Series B*, **268**, 1049–1053.
- Setchell, J. M. 2003. Behavioural development in male mandrills (*Mandrillus sphinx*): puberty to adulthood. *Behaviour*, **140**, 1053–1089.
- Setchell, J. M. & Dixson, A. F. 2002. Developmental variables and dominance rank in adolescent male mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, **56**, 9–25.
- Short, R. V., Mann, T. & Hay, M. F. 1967. Male reproductive organs of the African elephant, *Loxodonta africana*. *Journal of Reproduction and Fertility*, **13**, 517–536.
- Siegel, S. & Castellan, N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Slotow, R. & van Dyk, G. 2001. Role of delinquent young “orphan” male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. *Koedoe*, **44**, 85–94.
- Slotow, R., van Dyk, G., Poole, J., Page, B. & Klocke, A. 2000. Older bull elephants control young males. *Nature*, **408**, 425–426.
- Slotow, R., Balfour, D. & Howison, O. 2001. Killing of black and white rhinoceroses by African elephants in Hluhluwe–Umfolozo Park, South Africa. *Pachyderm*, **31**, 14–20.
- Sommer, V. & Mendoza-Granados, D. 1995. Play as an indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethology*, **99**, 177–192.
- Stamps, J. A. 1987. Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *American Naturalist*, **129**, 629–642.
- Viljoen, P. J. 1989. Habitat selection and preferred food plants of a desert-dwelling elephant population in the northern Namib Desert, South West Africa/Namibia. *African Journal of Ecology*, **27**, 227–240.
- Walters, J. R. 1987. Transition to adulthood. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 358–369. Chicago: University of Chicago Press.
- Watson, D. M. 1998. Kangaroos at play: play behaviour in the Macropodoidea. In: *Animal Play: Evolutionary, Comparative, and Ecological Perspectives* (Ed. by M. Bekoff & J. A. Byers), pp. 61–95. Cambridge: Cambridge University Press.
- Western, D., Moss, C. & Georgiadis, N. 1983. Age estimation and population age structure of elephants from footprint dimensions. *Journal of Wildlife Management*, **47**, 1192–1197.
- Whitehead, H. & Weilgart, L. 2000. The sperm whale—social females and roving males. In: *Cetacean Societies: Field Studies of Dolphins and Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 154–172. Chicago: University of Chicago Press.