Leadership in elephants: the adaptive value of age

Karen McComb[1,*,†], **Graeme Shannon**[1,4,*,†], **Sarah M. Durant**[2],
Katito Sayialel[3], **Rob Slotow**[4], **Joyce Poole**[3,5] **and Cynthia Moss**[3]

[1]*Mammal Vocal Communication and Cognition Research, School of Psychology, University of Sussex, Brighton BN1 9QH, UK*
[2]*Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK*
[3]*Amboseli Elephant Research Project, Amboseli Trust for Elephants, PO Box 15135, Langata 00509, Nairobi, Kenya*
[4]*Amarula Elephant Research Programme, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag X54001, Durban 4000, South Africa*
[5]*ElephantVoices, Buskhellinga 3, 3236 Sandefjord, Norway*

The value of age is well recognized in human societies, where older individuals often emerge as leaders in tasks requiring specialized knowledge, but what part do such individuals play in other social species? Despite growing interest in how effective leadership might be achieved in animal social systems, the specific role that older leaders may play in decision-making has rarely been experimentally investigated. Here, we use a novel playback paradigm to demonstrate that in African elephants (*Loxodonta africana*), age affects the ability of matriarchs to make ecologically relevant decisions in a domain critical to survival—the assessment of predatory threat. While groups consistently adjust their defensive behaviour to the greater threat of three roaring lions versus one, families with younger matriarchs typically under-react to roars from male lions despite the severe danger they represent. Sensitivity to this key threat increases with matriarch age and is greatest for the oldest matriarchs, who are likely to have accumulated the most experience. Our study provides the first empirical evidence that individuals within a social group may derive significant benefits from the influence of an older leader because of their enhanced ability to make crucial decisions about predatory threat, generating important insights into selection for longevity in cognitively advanced social mammals.

Keywords: leadership; cognitive abilities; playback experiment; social mammals; longevity; *Loxodonta africana*

1. INTRODUCTION

Despite theoretical predictions that democratic decision-making should predominate in animal groups [1–4], it is becoming clear that specific leaders commonly appear to guide the actions of other group members [5–8]. Leaders are therefore increasingly seen as important in coordinating social organization, and there is now growing interest in parallels between leadership in humans and animals that suggest common evolutionary origins, with the same morphological and behavioural traits predicting leadership across species [3]. Understanding the benefits to individual group members of accepting a leader's decision is critical to uncovering the evolutionary basis of leadership, and hence increasing our knowledge of the role leaders play in human and animal societies [3,9]. One situation in which individuals may gain from following a leader is if older leaders possess some form of superior knowledge enabling better decisions in response to environmental or social triggers [10–12].

Mathematical models of group decision-making have indicated that it may pay individuals in small groups to accept the decision of a knowledgeable leader where large disparities exist in the information possessed by different group members [1]. Indeed, research on humans indicates that age is correlated with leadership in domains that require specialized knowledge [13], and there is recent evidence that decisions about social conflicts improve with age despite declines in many forms of cognitive processing [14]. In animal societies, it has most often been suggested that older leaders provide a vital source of ecological knowledge (e.g. about the location of scarce resources or migration routes), but direct tests of this in natural populations are lacking because of the difficulties in quantifying the relevant skills [6,11,15,16].

A key facet of ecological knowledge that is more amenable to experimental investigation is the ability to respond appropriately to the threat of predators. Moreover, as anti-predator response strategies are often costly and may involve an element of risk [17], the experience to discern when such strategies should be implemented would have critical energetic and survival benefits for individual group members. By using a novel playback paradigm where lion roars were broadcast to simulate varying levels of predatory threat—presented by different numbers and sexes of lions—we were able to investigate

*Authors for correspondence (karenm@sussex.ac.uk; g.shannon@sussex.ac.uk).
†These authors contributed equally to the study.

1

directly how groups of African elephants (*Loxodonta africana*) with leaders of different ages performed at assessing fine-scaled differences in the risk involved. In doing so, we built on techniques previously developed to assess the factors affecting social knowledge in elephant groups [10].

Female African elephants live in matrilineal family units led by the oldest female, or matriarch, who plays a key role in coordinating group movements and responses to threat [10,18–20]. Other than humans, lions are the main natural predators of African elephants [21–23], typically preying on calves of less than 4 years of age [23,24]. Although it is often assumed that lionesses do most of the hunting, male lions are in fact considerably more effective and successful predators when it comes to targeting the largest prey—namely elephants and buffalo [23,25,26]. These large-bodied species often react to lion attacks with cooperative and aggressive defence mechanisms, presenting formidable opponents given their combined strength and dangerous weaponry [25,27]. In such situations, male lions, being on average 50 per cent larger in body mass and considerably more powerful than females [28], are at a distinct advantage. It is notable that the mean group size for successful male lion hunts on elephants is dramatically smaller than that for successful female hunts (1.8 versus 7 in one key study [23]), a finding also reflected in data on lion hunts of buffalo [25]. Moreover, while hunting success typically increases with group size [22,23], it has been demonstrated that male lions have the capability of overpowering a young elephant even when hunting alone [19,23]. Older elephant matriarchs should be more experienced in facing lion encounters than younger matriarchs, and hence we might expect them to be better able to identify the greater risk posed by larger groups of lions and by male lions in particular. Our study, using individually known elephants in Amboseli National Park, Kenya (see §2), provides an unusual opportunity to examine directly how the age of a leader may influence this vital ecological knowledge in a wild population.

Abilities to discriminate between different levels of predatory threat were tested by giving elephant family units playbacks of three lions versus a single lion roaring and, within these categories, roaring from male versus female lions (see §2). In a wide range of social species, individuals may benefit through increased attentiveness, group-defensive behaviour and, in some cases, even approaches to harass predators (mobbing), which can serve both to directly discourage attack and to gain further information about the threat involved [19,29,30]. While mobbing is not widespread among mammals [17], elephants are sufficiently large and well coordinated to search out and direct group attacks on potential predators [19,27,31]. In conjunction with our previous research on social knowledge in African elephants [10], we predicted that groups led by older matriarchs would show greater attentiveness, defensive bunching behaviour and increased likelihood of mobbing approach when faced with lion groups (as opposed to singletons) and with males (as opposed to females).

2. MATERIAL AND METHODS
(a) *Study population*
All playback experiments were conducted on a natural population of African elephants in Amboseli National Park in Kenya between May 2007 and July 2009. This study population encompasses approximately 1500 elephants, with 58 distinct family groups. The Amboseli Elephant Research Project (AERP; http://www.elephanttrust.org) has long-term demographic and behavioural data on the entire population, including detailed ages for all elephants born after 1971, while ages for older individuals were estimated using criteria that are accepted as standard in studies of African elephants [18,32]. All elephants in the population are habituated to the presence of AERP research vehicles.

(b) *Playback procedure*
A total of 72 playbacks were conducted on 39 elephant family groups (1–4 playbacks per group), with a mean of five adults (± 2.6 s.d.) in each family. All of the playbacks were carried out between 16.00 and 19.00 h, the time at which lions become active.

The lion roars used in the study had been recorded in the Serengeti National Park, Tanzania using Sennheiser MKH816T microphones and Panasonic SV-250 digital audio tape recorders [33,34]. Eight different playback exemplars were presented, consisting of two matched pairs of one lion versus three lions roaring for both male and female lions [33,34].

In each playback, a single bout of lion roars (mean duration: males, 39 ± 7 s; females, 40 ± 5 s) was broadcast to the subjects from a fieldwork vehicle that was located 100 m from the periphery of the family group. The lion roars were played through custom-built loudspeakers manufactured by Bowers & Wilkins, Steyning, UK and Intersonics Inc., Northbrook, IL, USA. The Bowers & Wilkins loudspeaker was powered by Alpine PDX-1.1000 and MRP-T222 amplifiers and the Intersonics loudspeaker by a Kenwood KAC-PS400M amplifier. In all playbacks the peak sound pressure level at 1 m from the loudspeaker was standardized at 116 dB, comparable with that of natural lion roars [33]. Sound pressure levels were measured with a CEL-414/3 sound level meter.

The first exemplars played to family groups were randomized; repeat playbacks for each sex of lion were then systematically paired with the first exemplars presented, so that across playbacks two factors (number of lions and sex of lion) were systematically varied in turn, while holding others constant. To avoid habituation, a minimum period of 7 days was left between playbacks to the same family. Playbacks were not given to groups with calves of less than one month as our previous work had indicated that the presence of such very young calves may result in abnormally high sensitivity to perceived threats over this short time period [10].

The behavioural responses of the elephants to playback were observed through binoculars and recorded on video, alongside live commentary, using a Canon XM2 video camera. From video analysis, we assessed five key behavioural measures that described the responses of the family group with particular reference to the matriarch (developed from [10]):

— *Matriarch prolonged listening*. Matriarch continues to exhibit evidence of listening response for more than 3 min after playback, where ears are held in a stiff extended position, often with the head slightly raised.
— *Matriarch bunching*. Defensive response to perceived threat by adult females (including the matriarch) and their young, which results in the diameter of the family

group decreasing after the broadcast of the playback stimulus (calculated in terms of elephant body lengths).

— *Matriarch bunching intensity.* The rate at which a defensive bunch of adult females (including the matriarch) and their young occurs. This measure classifies the overall level of threat response, scoring bunching intensity on a 4-point scale as follows:

(i) 0: No bunching occurred.

(ii) 1: Subtle reduction in the diameter of the group, elephants remain relaxed and continue with pre-playback behaviours (>3 min for bunch formation).

(iii) 2: Group forms a coordinated bunch, pre-playback behaviours such as feeding interrupted (1–3 min for bunch formation).

(iv) 3: Fast and sudden reduction in the diameter of the group, elephants very alert (<1 min for bunch formation).

— *Matriarch approach.* Distinct change in the direction and approach of the matriarch towards the source of playback.

— *Group to matriarch.* Adult females and/or their young respond to playback by moving towards the matriarch.

An independent observer who did not have access to the video commentary and was blind to the playback sequence second-coded 15 per cent of the video records; an overall agreement of 95 per cent was achieved on the binary response variables and the Spearman's ρ correlation on the scores for matriarch bunching intensity was 0.940 ($p < 0.001$). A video clip illustrating the highest level of bunching and mobbing approach is available as electronic supplementary material S1.

(c) *Statistical analyses*

The data were analysed using generalized linear mixed models (GLMMs) in R (www.r-project.org). To test the responses of elephants to lion playbacks as a function of predatory threat (number and sex of the lions) and the age of the matriarch, five key behaviours were used as dependent variables (see above), while the identity of the elephant group was entered as a random factor. Model selection was performed using Akaike's information criterion (AIC) [35], with lower AIC scores indicating better models; however, a more complex model with more degrees of freedom was only selected over a simpler model when the AIC differed by 2 or more [35]. In our main analysis, matriarch age was entered as a continuous variable in each of the GLMMs. A second analysis compared the behavioural responses of the oldest age class of matriarchs (≥ 60 years) with those ≤ 59 years. In all analyses, potentially confounding variables—the number of adult female elephants in the group and their average age [10]—were excluded during model selection as they generated higher AIC scores, with no significant main effects for the variables nor for interactions between them and the sex and number of lions.

3. RESULTS

In all cases, the best model (see §2) to describe the responses of elephants to playbacks included the number of lions, lion sex, matriarch age, and the interaction between lion sex and matriarch age (electronic supplementary material S2). The number of lions had significant effects on four out of five of our behavioural measures, with playback of three lions generating elevated responses as predicted (table 1 and figure 1). The ability to make this

basic distinction did not depend on the age of the matriarch, with no significant interactions occurring between matriarch age and the number of lions for any of our response variables. However, matriarch age (entered as a continuous variable) had marked effects on behaviour in response to playbacks of male versus female lions, with significant interactions between age of matriarch and sex of lions (electronic supplementary material S2 and table 1). More specifically, sensitivity to male (versus female) lions increased with matriarch age, matriarchs being more likely to engage in prolonged listening and defensive bunching, and showing a higher bunching intensity when faced with male lion roars as they get older (table 1 and figure 2a; see electronic supplementary material S3 for scatter plots of raw data). Groups with older matriarchs were also more likely to approach the source of playback when male roars were presented (table 1 and figure 2b). In addition, as reproductive activity shows a marked decline in female elephants between the ages of 55 and 60 years [18,36,37], we investigated the sensitivity of the oldest age class (60 years and above) to the particular threat posed by male lions in a secondary analysis. Comparing these with matriarchs of 59 years and younger (matriarch age was categorical in this analysis: age ≤ 59, $n = 53$; age 60+, $n = 19$), there were significant interactions between matriarch age class and lion sex in our measures of attentiveness and defensive bunching (table 1). The oldest matriarchs were more likely to engage in prolonged periods of listening and exhibited greater defensive bunching (higher probability of bunching and greater bunching intensity) in response to male versus female roars, demonstrating their key role in identifying and responding to this most serious threat (table 1 and figure 2c,d). Other potentially confounding variables—number of females in the group and mean age of females other than the matriarch—were excluded from the final models because their inclusion produced poorer results when model selection was carried out using AIC scores (see §2).

4. DISCUSSION

These results demonstrate that while elephant family groups react more strongly to three lions than a single lion roaring irrespective of matriarch age, those led by older matriarchs show a greater sensitivity to the more serious threat posed by male lions across all our behavioural responses, including measures of attentiveness, bunching and mobbing approach. The superior ability to detect the presence of male lions at an early stage—evident in the greater probability of older matriarchs engaging in prolonged periods of listening and defensively bunching with their groups—is likely to have significant survival benefits affording better protection for vulnerable calves in particular. Previous researchers have speculated that elephant groups can derive fitness benefits from the improvement in ecological knowledge conferred by an older matriarch, suggesting that this enables better utilization of scarce resources and predator avoidance during periods of drought [15]. Our work provides the first direct experimental evidence that older matriarchs are in fact able to make better decisions when faced with ecological challenges—in this case, the presence of dangerous predators. It thus bridges an important gap between

Table 1. Results of GLMMs investigating matriarch behavioural responses to lion roar playbacks (*a*) with matriarch age entered as a continuous variable and (*b*) with two age classes of matriarchs—the oldest age class (60 years and over) and all younger matriarchs (≤59 years).

dependent variable	parameters	estimate	s.e.	Z-value	p-value
(*a*)					
matriarch prolonged listening	lion number	1.128	0.336	3.357	0.0008
	lion sex	−5.897	2.903	−2.031	0.04
	matriarch age	−0.005	0.032	−0.157	0.88
	lion sex × matriarch age	0.102	0.054	1.890	0.06
matriarch bunching	lion number	1.237	0.329	3.758	0.0002
	lion sex	−9.567	3.095	−3.091	0.002
	matriarch age	−0.034	0.031	−1.092	0.27
	lion sex × matriarch age	0.166	0.058	2.862	0.004
matriarch bunching intensity	lion number	0.565	0.148	3.814	0.0001
	lion sex	−5.554	1.503	−3.695	0.0002
	matriarch age	−0.014	0.013	−1.113	0.27
	lion sex × matriarch age	0.094	0.026	3.589	0.0003
matriarch approach	lion number	0.076	0.359	0.211	0.83
	lion sex	−7.020	3.780	−1.857	0.06
	matriarch age	−0.030	0.045	−0.659	0.51
	lion sex × matriarch age	0.148	0.070	2.114	0.03
group to matriarch	lion number	1.269	0.375	3.387	0.0007
	lion sex	−6.258	3.053	−2.050	0.04
	matriarch age	−0.007	0.034	−0.219	0.83
	lion sex × matriarch age	0.115	0.057	2.011	0.04
(*b*)					
matriarch prolonged listening	lion number	1.991	0.363	3.302	0.001
	lion sex	−4.808	2.028	−2.370	0.02
	matriarch age class	−0.874	0.962	−0.909	0.36
	lion sex × matriarch age class	3.234	1.457	2.221	0.03
matriarch bunching	lion number	1.279	0.351	3.635	0.0003
	lion sex	−6.597	2.137	−3.088	0.002
	matriarch age class	−1.374	0.965	−1.424	0.15
	lion sex × matriarch age class	4.194	1.532	2.739	0.006
matriarch bunching intensity	lion number	0.542	0.152	3.567	0.0004
	lion sex	−3.016	0.900	−3.350	0.0008
	matriarch age class	−0.409	0.401	−1.020	0.31
	lion sex × matriarch age class	1.825	0.593	3.079	0.002
matriarch approach	lion number	0.028	0.346	0.081	0.94
	lion sex	−1.723	2.139	−0.806	0.42
	matriarch age class	−0.083	1.220	−0.068	0.95
	lion sex × matriarch age class	1.850	1.522	1.216	0.22
group to matriarch	lion number	1.174	0.364	3.224	0.001
	lion sex	−0.361	1.826	−0.198	0.84
	matriarch age class	0.406	0.913	0.444	0.66
	lion sex × matriarch age class	0.042	1.326	0.032	0.98

theoretical predictions about how knowledge might be expected to affect leadership [1,9] and empirical studies, which to date have been largely confined to observational accounts [6,7,15].

It has recently been suggested that prey species with large brains relative to their body size may be better at evading predators because they can more effectively adjust their behavioural responses to specific encounters [38]. Our results indicate that elephants can indeed make important distinctions between threat levels even within a predator class, in parallel with research showing their ability to distinguish human ethnic groups that pose different levels of threat on the basis of olfactory and visual cues [39]. Moreover, the results demonstrate how the accumulated knowledge of the oldest individuals may have an over-

riding influence on the effectiveness of anti-predator decisions made by the social group as a whole, and they highlight the vital role of such individuals in natural populations [10]. This is a particularly important consideration where relatively large-brained social species have the opportunity to accumulate ecological information over long lifespans and considerable disparities in knowledge between different individuals are therefore likely to arise.

While we cannot be sure that matriarch age will correlate with experience of lions in every instance, it is reasonable to assume that as matriarchs get older they will accumulate exposure to the particular risks posed by lions. Although elephants are relatively impregnable to most predators by virtue of their large body size and aggressive group defence, lions remain a very significant
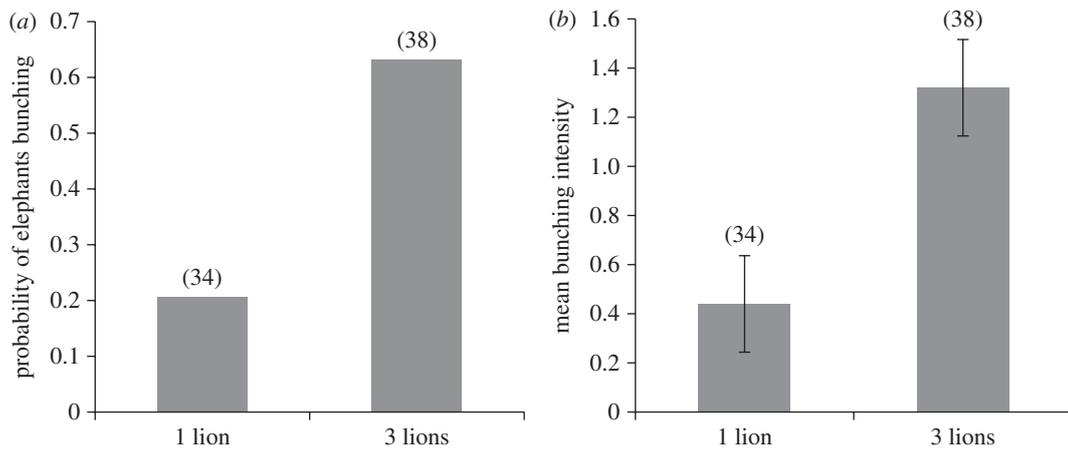
Figure 1. Elephant response to the scale of predation threat as simulated by one versus three roaring lions: (*a*) probability of matriarch bunching and (*b*) matriarch bunching intensity (mean ± s.e.m.). Number of playbacks given in parentheses.
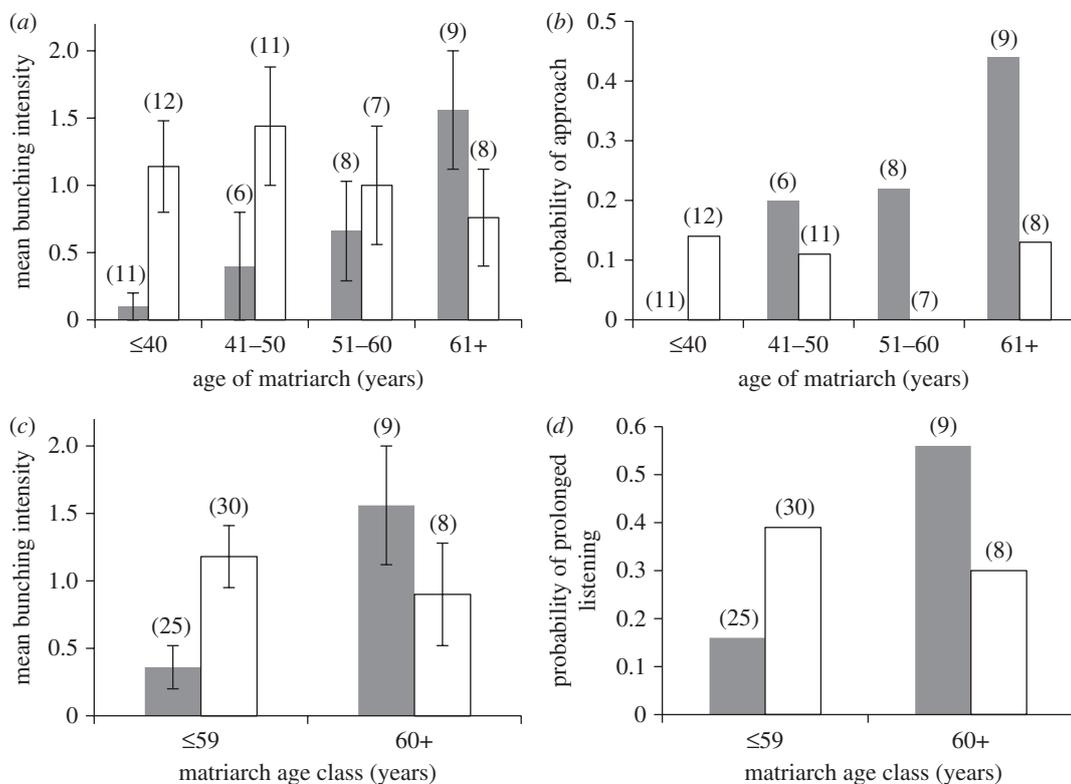

Figure 2. Behavioural responses of matriarchs and their family groups to male (grey bars) versus female (white bars) lions depicted as a function of increasing matriarch age for illustration (see table 1 for detailed analysis and electronic supplementary material S3 for raw data). (*a,c*) Mean bunching intensity (±s.e.m.); (*b*) probability of approach; and (*d*) probability of prolonged listening. Number of playbacks given in parentheses.

threat and have the potential to shape the evolution of specific anti-predator behaviour [23,27]. Despite this, the occurrence of lion predation on elephants is typically a rare event [24]. Moreover, the sex ratio of adult lions in most populations is heavily female-biased [40,41], with a 1 M : 1.8 F ratio in the Amboseli population [42], which may lower the exposure to male-specific cues further still. Our experiments test elephant abilities to make a rather subtle distinction—between characteristics defining male and female roars—and while sex-specific acoustic differences have been documented in lion roars [43], these are not overtly obvious to human listeners. It is perhaps not surprising therefore that considerable experience,

built up over a long lifespan, should enable older individuals to perform better in this task.

In common with humans and certain other social animals, in particular pilot and killer whales, female elephants can have a significant post-reproductive life-span—although it is currently unclear whether they exhibit menopause [18,37,44,45]. While reproductive activity declines among this oldest age class, they show no signs of increased vulnerability to predators, and in fact are often the largest individuals within family groups [31]. Indeed, our results suggest that this oldest age class of females can provide significant benefits for their groups in the context of decision-making about

predators. As a result of typically no longer having young offspring, they may be able to take a more active role in group defence and could be more attentive to ecological signals. However, if families with older matriarchs were simply more reactive, we would predict an overall increase in sensitivity to lion roars rather than the greater differential response to male versus female roars reported here. Instead, older matriarchs appear more adept at associating male lion roars with a greater level of threat. Observational data also indicate that it is individuals of 60 years and older who have the greatest success in leading large-scale foraging movements [16]—again suggesting that in decisions relating to ecological knowledge, the level of experience that these oldest individuals possess may prove critical. Recent research on humans has demonstrated the key role that grandmothers can play in enhancing the reproductive success of their offspring by assisting in child-rearing after their own reproduction has ceased [46,47]. Our findings indicate that through their greater ecological knowledge, older females can also represent a crucial resource in other long-lived cognitively advanced mammals that live in kin-based social groups.

Leadership is known to be crucial in the coordination of human groups, but we are only now beginning to appreciate its role in animal societies [3,4]. In order to fully understand how animal groups are organized and achieve collective action, it is vital to determine the advantages that a leader may bring to group decision-making. Our study provides the first empirical evidence that individuals within a social group may benefit directly from the influence of an older leader because of their enhanced ability to make crucial decisions about predatory threat. It thus generates important insights into selection for longevity and the evolution of a sophisticated social structure that supports the coordinating role of a single older leader. Such abilities are likely to be highly relevant in other large-brained, long-lived social species where older individuals play a key role in coordinating group activities.

REFERENCES

1 Conradt, L. & Roper, T. J. 2003 Group decision-making in animals. *Nature* **421**, 155–158. (doi:10.1038/nature01294)

2 Conradt, L., Krause, J., Couzin, I. D. & Roper, T. J. 2009 'Leading according to need' in self-organizing groups. *Am. Nat.* **173**, 305–312. (doi:10.1086/596532)

3 King, A. J., Johnson, D. D. P. & Van Vugt, M. 2009 The origins and evolution of leadership. *Curr. Biol.* **19**, 911–916. (doi:10.1016/j.cub.2009.07.027)

4 King, A. J. 2010 Follow me! I'm a leader if you do; I'm a failed initiator if you don't? *Behav. Proc.* **84**, 671–674. (doi:10.1016/j.beproc.2010.03.006)

5 King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlishaw, G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)

6 Maransky, B. P. & Bildstein, K. L. 2001 Follow your elders: age related differences in the migration behavior of broad-winged hawks at hawk mountain sanctuary, Pennsylvania. *Wilson Bull.* **113**, 350–353. (doi:10.1676/0043-5643(2001)113[0350:FYEARD]2.0.CO;2)

7 Wright, R., Stone, R. E. & Brown, N. 2003 Communal roosts as structured information centres in the raven, *Corvus corax*. *J. Anim. Ecol.* **72**, 1003–1014. (doi:10.1046/j.1365-2656.2003.00771.x)

8 Lusseau, D. & Conradt, L. 2009 The emergence of unshared consensus decisions in bottlenose dolphins. *Behav. Ecol. Sociobiol.* **63**, 1067–1077. (doi:10.1007/s00265-009-0740-7)

9 Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

10 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. (doi:10.1126/science.1057895)

11 Greve, W., Kierdorf, H. & Kierdorf, U. 2009 The Akela effect—is there an evolutionary benefit from senators in mammals? *Biol. Hyp.* **2**, 213–216.

12 McAuliffe, K. & Whitehead, H. 2005 Eusociality, menopause and information in matrilineal whales. *Trends Ecol. Evol.* **20**, 650. (doi:10.1016/j.tree.2005.09.003)

13 Van Vugt, M. 2006 Evolutionary origins of leadership and followership. *Pers. Soc. Psychol. Rev.* **10**, 354–371. (doi:10.1207/s15327957pspr1004_5)

14 Grossmann, I., Na, J., Varnum, M. E. W., Park, D. C., Kitayama, S. & Nisbett, R. E. 2010 Reasoning about social conflicts improves into old age. *Proc. Natl Acad. Sci. USA* **107**, 7246–7250. (doi:10.1073/pnas.1001715107)

15 Foley, C., Pettorelli, N. & Foley, L. 2008 Severe drought and calf survival in elephants. *Biol. Lett.* **4**, 541–544. (doi:10.1098/rsbl.2008.0370)

16 Mutinda, H., Poole, J. H. & Moss, C. J. 2011 Decision-making and leadership in using the ecosystem. In *The Amboseli elephants: a long-term perspective on a long-lived mammal* (eds C. J. Moss, H. Croze & P. C. Lee), pp. 246–259. Chicago, IL: The University of Chicago Press.

17 Caro, T. 2005 *Antipredator defenses in birds and mammals*. Chicago, IL: The University of Chicago Press.

18 Moss, C. 2001 The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *J. Zool. (Lond.)* **255**, 145–156. (doi:10.1017/S0952836901001212)

19 Douglas-Hamilton, I. 1972 The ecology and behaviour of the African elephant: the elephants of Lake Manyara. PhD thesis, University of Oxford, Oxford, UK

20 Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M. 2005 The socio-ecology of elephants: analysis of the processes creating multileveled societies. *Anim. Behav.* **69**, 1357–1371. (doi:10.1016/j.anbehav.2004.08.018)

21 Joubert, D. 2006 Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. *Afr. J. Ecol.* **44**, 279–281. (doi:10.1111/j.1365-2028.2006.00626.x)

22 Power, R. J. & Compion, R. X. S. 2009 Lion predation on elephants in the Savuti, Chobe National Park, Botswana. *Afr. Zool.* **44**, 36–44. (doi:10.3377/004.044.0104)

23 Loveridge, A. J., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. 2006 Influence of drought predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J. Zool. (Lond.)* **270**, 523–530. (doi:10.1111/j.1469-7998.2006.00181.x)

24 Ruggiero, R. G. 1991 Opportunistic predation on elephant calves. *Afr. J. Ecol.* **29**, 86–89. (doi:10.1111/j.1365-2028.1991.tb00823.x)

25 Funston, P. J., Mills, M. G. L. & Biggs, H. C. 2001 Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool. (Lond.)* **253**, 419–431. (doi:10.1017/S0952836901000395)

26 Funston, P. J., Mills, M. G. L., Biggs, H. C. & Richardson, P. R. K. 1998 Hunting by male lions: ecological influences and socioecological implications. *Anim. Behav.* **56**, 1333–1345. (doi:10.1006/anbe.1998.0884)

27 Owen-Smith, R. N. 1992 *Megaherbivores: the influence of very large body size on ecology.* Cambridge, UK: Cambridge University Press.

28 Smuts, G. L., Robinson, G. A. & Whyte, I. J. 1980 Comparative growth of wild male and female lions (*Panthera leo*). *J. Zool. (Lond.)* **190**, 365–373. (doi:10.1111/j.1469-7998.1980.tb01433.x)

29 Graw, B. & Manser, M. 2007 The function of mobbing in cooperative meerkats. *Anim. Behav.* **74**, 507–517. (doi:10.1016/j.anbehav.2006.11.021)

30 Caro, T. M., Graham, C. M., Stoner, C. J. & Vargas, J. K. 2004 Adaptive significance of antipredator behaviour in artiodactyls. *Anim. Behav.* **67**, 205–228. (doi:10.1016/j.anbehav.2002.12.007)

31 Moss, C. 1988 *Elephant memories.* Chicago, IL: The University of Chicago Press.

32 Moss, C. 1996 Getting to know a population. In *Studying elephants* (ed. K. Kangwana), pp. 58–74. Nairobi, Kenya: African Wildlife Foundation.

33 McComb, K., Packer, C. & Pusey, A. 1994 Roaring and numerical assessment in contests between groups of female lions, *Panthera leo. Anim. Behav.* **47**, 379–387. (doi:10.1006/anbe.1994.1052)

34 Grinnell, J. & McComb, K. 1996 Female grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. *Behav. Ecol.* **7**, 55–59. (doi:10.1093/beheco/7.1.55)

35 Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach.* New York, NY: Springer.

36 Freeman, E. W., Whyte, I. & Brown, J. 2008 Reproductive evaluation of elephants culled in Kruger National Park, South Africa between 1975 and 1995. *Afr. J. Ecol.* **47**, 192–201. (doi:10.1111/j.1365-2028.2008.00957.x)

37 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, UK: Clarendon Press.

38 Shultz, S. & Dunbar, R. I. M. 2006 Chimpanzee and felid diet composition is influenced by prey brain size. *Biol. Lett.* **2**, 505–508. (doi:10.1098/rsbl.2006.0519)

39 Bates, L., Sayialel, K. N., Njiraini, N. W., Moss, C. J., Poole, J. H. & Byrne, R. W. 2007 Elephants classify human ethnic groups by odor and garment color. *Curr. Biol.* **17**, 1938–1942. (doi:10.1016/j.cub.2007.09.060)

40 Creel, S. & Creel, N. M. 1997 Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and off take. *Afr. J. Ecol.* **35**, 83–93. (doi:10.1111/j.1365-2028.1997.062-89062.x)

41 Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. & Borgerhoff-Mulder, M. 1988 Reproductive success of lions. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 363–383. Chicago, IL: University of Chicago Press.

42 van der Werf, M. 2008 Lions (*Panthera leo*) of Amboseli National Park: a study on lion ecology in relation to conflict with livestock owners. Master's thesis, University of Leiden, The Netherlands.

43 Pfefferle, D., West, P. M., Grinnell, J., Packer, C. & Fischer, J. 2006 Do acoustic features of lion, *Panthera leo*, roars reflect sex and male condition? *J. Acoust. Soc. Am.* **121**, 3947–3953. (doi:10.1121/1.2722507)

44 Johnstone, R. A. & Cant, M. A. 2010 The evolution of menopause in cetaceans and humans: the role of demography. *Proc. R. Soc. B* **277**, 3765–3771. (doi:10.1098/rspb.2010.0988)

45 Sukumar, R. 1992 *The Asian elephant.* Cambridge, UK: Cambridge University Press.

46 Lahdenperä, M., Lummaa, V., Helle, S., Tremblay, M. & Russel, A. F. 2004 Fitness benefits of prolonged reproductive lifespan in women. *Nature* **428**, 178–181. (doi:10.1038/nature02367)

47 Shanley, D. P., Sear, R., Mace, R. & Kirkwood, T. B. L. 2007 Testing evolutionary theories of menopause. *Proc. R. Soc. B* **274**, 2943–2949. (doi:10.1098/rspb.2007.1028)