

accurately in Eros latitude and longitude (4). Several cases have been found where the laser illuminated a boulder at almost the same time as when an image was obtained, yielding a feature in the NLR profile and an almost simultaneous image in which the boulder can be identified. These cases yield NLR boresight determinations to within an ~2-pixel uncertainty within the image frame (7). During the low-altitude flyover, the NLR boresight was located at line = 220, sample = 255, in the rectified MSI pixel format (8), where the full frame has 412 lines and 537 samples and where each pixel is square and subtends 95.9 μ rad. Once the boresight alignment of the NLR is determined in relation to the MSI, each of these coordinated data sets enhances the interpretation of the other. The MSI helps to characterize topographic features detected by the NLR, e.g., by distinguishing between grooves and craters. The NLR helps to distinguish brightness variations caused by topography from those caused by differences in reflectivity.

7. A. F. Cheng et al., *Icarus* **148**, 572 (2000).
8. S. Murchie et al., *Icarus* **140**, 66 (1999).
9. J. Veverka et al., *Science* **292**, 484 (2001); J. Veverka et al., *Science* **289**, 2088 (2000).
10. Locations on the asteroid surface are specified in a planetocentric system referenced to the center of mass (4). The closest approach observations could not be targeted to any specific surface feature because of navigational uncertainty.
11. Elevation is determined in relation to the potential arising from the mass of the asteroid and the centrifugal potential, or geopotential, given by

$$\Phi(\mathbf{x}) = - \int d^3\mathbf{x}' \frac{G\rho}{|\mathbf{x} - \mathbf{x}'|} - \frac{\Omega^2 r^2}{2}$$

where the gravitational potential at $\mathbf{x}$ is found from an integral over the volume of the asteroid, r is the distance from the point $\mathbf{x}$ to the rotation axis, and Ω is the rotation rate $3.31166 \times 10^{-4} \text{ rad s}^{-1}$ (4, 7). The geopotential is determined by numerical integration over the volume of Eros assuming a constant density (4). The geopotential height h measured in meters is defined by (27)

$$h(\mathbf{x}_i) = |\Phi(\mathbf{x}_i)/g_{\text{avg}}|$$

Hence $h(\mathbf{x})$ is proportional to geopotential but is scaled by a factor g_{avg} , the local average magnitude of the effective gravitational acceleration over a short track, typically <1 km in length. The later track in Fig. 1 was analyzed in six segments that were concatenated.

12. Distance is defined with the line that is the least squares best fit to a short track of laser spots in three dimensions. The position of each laser spot is projected onto this line, and distance is measured along the line. Distance is determined independently for each of the six segments concatenated to form the later track in Fig. 1 (upper right inset). The slope between two samples is not determined with this projected distance; slope is determined from the geopotential height difference and the magnitude of the displacement vector. Hence the slope is not simply related to the graphical slopes of the curves in the insets to Fig. 1.
13. The area-weighted slope distribution refers to slopes in three dimensions and, specifically, the angle α between the local effective gravity and the inward surface normal. The NLR measures slopes along a track that can be approximated as linear for a short distance. If the track is oriented randomly within the local tangent plane to the surface, then the slope along the track α_T (the angle between the track and the local horizontal plane, perpendicular to the local gravity) is related statistically to the slope in three dimensions. Specifically, the two slopes are related on the average by $(\sin \alpha_T / \sin \alpha) = 2/\pi$.
14. The depths of small fresh lunar craters are ~0.2 times the diameters [H. Melosh, *Impact Cratering: A Geologic Process* (Oxford Univ. Press, New York, 1989)].
15. Crater scaling relations (22) indicate that a 14-m block, which would have the same cross-sectional area as the block in the flat-floored crater, would

have created a crater of 190 m in diameter (assuming gravity scaling), given an impact velocity of 240 m s^{-1} . In such an impact, the projectile would be buried below the surface (23). On the other hand, if the block was ejected from an impact elsewhere on Eros, it impacted the surface below the escape velocity of 3 to 17 m s^{-1} (24) and would not necessarily fracture. At an impact velocity of 10 m s^{-1} , a crater of 64 m in diameter would be created.

16. D. Turcotte, *Fractals and Chaos in Geology and Geophysics* (Cambridge Univ. Press, New York, 1997). The fractal dimension D is related to the Hurst exponent H by $D = 2 - H$.
17. M. Shepard, B. Campbell, *Icarus* **134**, 279 (1998). The roughness of the terrestrial a'a lava cannot be extrapolated to scales >1 m in a fractal manner, because of the effect of competing physical processes in determining texture. It remains to be established whether roughness on Eros behaves fractally on scales as short as 1 m.
18. On-ridge intervals are as follows: 147953865 to 147953871 s, 147953884 to 147953889 s, 147953898 to 147953910 s, and 147953929 to 147953936 s. Off-ridge intervals are as follows: 147953871 to 147953877 s, 147953890 to 147953897 s, 147953911 to 147953929 s, and 147953936 to 147953941 s.
19. The depth of infill can be inferred by assuming that the depth of a fresh crater is 0.2 times the diameter. This argument gives ~20 m of infill for the flat-floored crater of Fig. 2. An alternative interpretation is that the flat bottom of the crater between points e and f is caused by the failure of the cratering event to excavate into a flat competent substrate (25). Laboratory impact experiments into a layered target, with an unconsolidated layer on top of a hard competent substrate, show that flat-bottomed craters form when the crater diameter is 8 to 10 times the depth of the unconsolidated layer, which would be 17 m deep in this interpretation. However, the crater morphology is more suggestive of mantling (9). A complication is that the flat-bottomed crater is situated within a larger depression that extends roughly from point d to a distance of 550 m in Fig. 2B, beyond point f. This larger depression is 370 m across along

the track, but only 40 m deep. The flat-bottomed crater and the larger depression around it may comprise a single impact crater, in which case the apparent rim at the level of points e and f could result from variation in the mechanical properties of the regolith with depth. Available evidence does not resolve this issue, but in any case, inferred regolith depths would be tens of meters, consistent with previous work (4, 7, 9). The original depth of a fresh 370-m crater would be ~74 m, and the flat crater floor could result from 34 m of infill or (less likely) from the presence of a hard competent substrate 40 m below the original surface.

20. Eros is currently in a chaotic orbit, which evolves on million-year time scales and which crosses the orbit of Mars and approaches that of Earth (26). The flux of impactors on Eros in its present orbit was calculated by a Monte Carlo method (27) with a projectile distribution in orbital elements as observed for minor planets, but a size distribution extrapolated downward to values relevant to cratering on asteroids [e.g., (28)]. In its present orbit, Eros would require 10^{10} years to reach equilibrium densities of craters >200 m (27), implying that most of the larger craters formed while Eros was still within the main belt (9).
21. P. Thomas et al., *Icarus* **107**, 23 (1994); P. Thomas et al., *Icarus* **120**, 20 (1996).
22. K. Holsapple, *Annu. Rev. Earth Planet. Sci.* **21**, 333 (1993).
23. W. K. Hartmann, *Icarus* **63**, 69 (1985).
24. D. K. Yeomans et al., *Science* **289**, 2085 (2000).
25. W. Quaide, V. Overbeck, *J. Geophys. Res.* **73**, 5247 (1968).
26. P. Michel, P. Farinella, C. Froeschle, *Astron. J.* **16**, 2023 (1998).
27. O. Barnouin-Jha, A. Cheng, *Lunar Planet. Sci.* **XXXI** (abstr. 1255) (2000) [CD-ROM].
28. R. Greenberg et al., *Icarus* **120**, 106 (1996).
29. The NLR and MSI investigations are supported by NASA under the NEAR-Shoemaker Project. We acknowledge the contributions of the spacecraft and mission operations teams.

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Matriarchs As Repositories of Social Knowledge in African Elephants

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Despite widespread interest in the evolution of social intelligence, little is known about how wild animals acquire and store information about social companions or whether individuals possessing enhanced social knowledge derive biological fitness benefits. Using playback experiments on African elephants (*Loxodonta africana*), we demonstrated that the possession of enhanced discriminatory abilities by the oldest individual in a group can influence the social knowledge of the group as a whole. These superior abilities for social discrimination may result in higher per capita reproductive success for female groups led by older individuals. Our findings imply that the removal of older, more experienced individuals, which are often targets for hunters because of their large size, could have serious consequences for endangered populations of advanced social mammals such as elephants and whales.

Although there is considerable interest in the evolution of social intelligence (1–4), we still know little about how wild animals gain and store information about social companions or whether the possession of superior social knowledge enhances fitness. When mammals

live in complex fission-fusion societies (5–7), individuals may encounter hundreds of others during their daily ranging patterns, and time intervals between repeated exposures to the same individuals may be extremely long. Under these circumstances, the problem of distin-

guishing genuine strangers from a wide range of more regular associates is far from trivial.

Female African elephants live in matrilineal family units led by the oldest female, or matriarch. Within our Kenyan study population, a single family unit directly encounters, on average, 25 other families in the course of a year, representing a total of around 175 adult females (8). Previous paired playbacks indicated that adult females are familiar with the contact calls of around 100 others in the population, being able to discriminate between calls on the basis of how often they associate with the caller (9). However, families differ in how good they are at this task. Here we assess the discriminatory abilities of particular families in detail as a way to investigate the causes and consequences of social knowledge acquisition. In particular, we test the hypothesis that family units with older matriarchs are superior at discriminating the calls of close associates from those of distant associates, statistically excluding other potential explanatory factors. We also examine the relationship between matriarch age and reproductive success, linking reproductive success to matriarch age and response to playbacks. This study provides an unusual opportunity to investigate the role that memory can play in the social behavior of a long-lived vertebrate species.

In our study population in Amboseli National Park, Kenya, data on life histories

and association patterns have been obtained for more than 1700 individual elephants over 28 years by the Amboseli Elephant Research Project (7, 9, 10). Vocal discrimination abilities were tested by giving each of 21 family units, over the course of 7 years, a series of playbacks (11) of contact calls from adult females in other families in the population with whom they had a range of association indices (12). Contact calls, which have infrasonic fundamental frequencies but harmonics that extend well into the audible range, are the most common call that adult females use to advertise their location to widely spaced social companions (9, 13). The probability of families of subjects bunching into defensive formation on hearing playbacks of calls from other families decreased with the association index with the caller, conforming to a logistic curve [logistic model on the binary variable of bunching (14): the effect of association index $\chi^2 = 15.30$, $df = 1$, $P < 0.001$]. This curve describes the probability of bunching as the association index increases, generally leveling to zero at high indices. The detection of the presence of less familiar females (low-association-index families) is potentially beneficial, because this section of the population is more likely to initiate agonistic disputes or harass young calves (9).

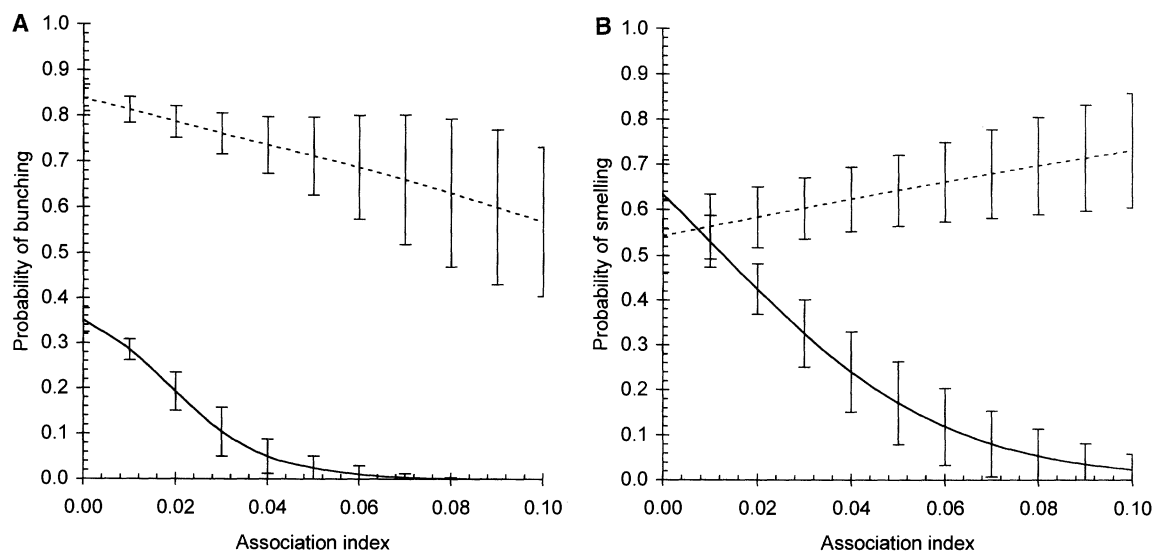
The age of the matriarch (10, 15) had a significant effect on the probability of bunching when controlling for the association index with the caller and family identity, and there was a significant interaction between the age of the matriarch and the association index (Table 1). Other potentially confounding variables—the number of females in the

group, the mean age of females other than the matriarch, the number of calves, the age of the youngest calf, and the presence or absence of adult males—were excluded from the model because their effects were not found to be statistically significant. The probability of bunching decreased with increasing matriarch age, suggesting that families with older matriarchs may have either larger networks of vocal recognition or greater social confidence than families with younger matriarchs. However, of greater importance with respect to our hypothesis was the interaction between the age of the matriarch and the association index with the caller. Specifically, the sensitivity of the bunching response to the association index increased with the age of the matriarch, so that families with older matriarchs were relatively much more reactive to females with whom they had a low association index than to those with whom they had a high association index (Table 1 and Fig. 1A). For example, although families with old matriarchs (55 years) were several thousand times more likely to bunch in response to calls from families with whom they had a low association index (0.01) than to those with whom they had a high association index (0.1), the probability of bunching for families with young matriarchs (35 years) increased only marginally ($\times 1.4$) across these conditions (Fig. 1A). If families with older matriarchs were simply more confident, we would predict their lower level of defensiveness overall but not these marked differences in the slope of the logistic curves. Rather, families with older matriarchs appear considerably more adept at using auditory signals to

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Fig. 1. The variation of response to playback calls as a function of the association index for families with matriarchs of differing ages. Values depicted are those from a logistic regression model (as described in Table 1) for families with matriarchs of 35 years (young matriarchs: dashed line) and matriarchs of 55 years (old matriarchs: solid line). Although age was a continuous variable throughout our analyses (the range of ages in our sample was 27 to 67 years), here we focus on two age groups that are representative of young and old matriarchs in order to clearly illustrate the interaction between the age of the matriarch and the association index with the caller. Standard error bars predicted from the models are depicted as a guide. The graphs describe probabilities of (A) bunching and (B) smelling.



REPORTS

correctly discriminate between familiar and unfamiliar females in the vicinity and respond appropriately.

Although bunching in response to a playback is primarily a defensive behavior, smelling must constitute a means of further exploration: When subjects smell after playbacks, they attempt to gather olfactory information on the caller's identity. An examination of the binary variable "smelling" in response to playbacks showed the same interaction between the age of the matriarch and the association index that characterized the bunching response (Table 1). Subjects in groups with older matriarchs were much more likely to use their trunks to smell if played calls from low- rather than high-associ-

ation-index families (Fig. 1B). In contrast, groups of subjects with younger matriarchs failed to show this relatively inflated probability of gathering olfactory information about infrequent associates. It is important to note that here families with older matriarchs were at least as reactive as families with younger matriarchs to callers with low association indices. However, their ability to distinguish between calls from low- and high-association-index families was apparently much greater.

Neither the smelling nor the bunching response was affected by the number or age of the other females in the group (Table 1), indicating that it is the matriarch who signals to the rest of her group whether defen-

sive or exploratory behavior is necessary. Although determining the mechanism by which the matriarch orchestrates this change in group behavior is not within the scope of the current study, a subtle acoustic or olfactory cue is the most likely possibility. There are anecdotal reports in the literature of females following the lead of their matriarch in other coordinated group activities (7, 13, 16).

The superior discriminatory abilities of older matriarchs should translate into reproductive benefits for the family unit, because time is more efficiently allocated by reserving defensive behavior for circumstances where it is appropriate, and because opportunities for cooperation with more frequent associates are provided. In support of this hypothesis, using an analysis that controlled for the number of females per family, the age of the matriarch was a significant predictor of the number of calves produced by the family per female reproductive year over the course of the study (17), our standardized measure of recent reproductive success (Table 2). Additional factors, including knowledge that older matriarchs had accumulated in a variety of other domains, might have contributed to this association. To explore the relationship between responses to playbacks and reproductive success more specifically, we calculated inflection points for the logistic curves of bunching and smelling on the association index for each family [as $-\alpha/\beta$, see (18)]. These were used as aggregate statistics describing between-family differences in response to playbacks. Entering these into an analysis of the residual variation in reproductive success after removing the variance due to the age of the matriarch (and the number of females) showed that families appeared to derive a reproductive benefit ($P = 0.05$ to 0.08) by bunching and smelling more readily; that is, by showing greater caution and exploratory behavior when presented with another female's call. Thus, it is likely that families with old matriarchs benefit reproductively because their matriarchs target caution at the appropriate individuals: callers that are strange to them. Also, the independent reproductive benefit from exhibiting more caution and exploratory behavior (once the effects of matriarch age have been removed) may explain why families that have young matriarchs, with their reduced social knowledge, show a greater overall tendency to bunch and smell.

Previous researchers have speculated that individuals can derive fitness benefits from an improvement in ecological knowledge that accompanies aging (19, 20). Our results suggest that aging may also influence reproductive success through its ef-

Table 1. Deviance tables obtained after fitting binary responses to playbacks to a logistic regression model.

Variable	Coefficient	Deviance*	df	Significance
<i>Bunching</i>				
Variables included in final model†				
Family‡	—	33.5	20	$P = 0.029$
Age of matriarch	−0.514	8.06	1	$P = 0.005$
Association index	98.0	2.11	1	$P = 0.147$
Age of matriarch $\times$ association index	−4.31	6.50	1	$P = 0.011$
Variables excluded from final model§				
Mean age of other females in group	−0.201	1.34	1	$P = 0.248$
Number of females in group	0.033	0.03	1	$P = 0.867$
Number of calves in group¶	0.015	0.00	1	$P = 0.946$
Age of youngest calf in group	0.032	1.69	1	$P = 0.194$
Presence or absence of adult males	−0.851	1.92	1	$P = 0.166$
<i>Smelling</i>				
Variables included in final model**				
Age of matriarch	0.0188	0.64	1	$P = 0.423$
Association index	97.2	7.74	1	$P = 0.005$
Age of matriarch $\times$ association index	−2.54	8.26	1	$P = 0.004$
Variables excluded from final model§				
Family‡	—	7.0	20	$P = 0.997$
Mean age of other females in group	0.0210	0.18	1	$P = 0.669$
Number of females in group	−0.0309	0.29	1	$P = 0.590$
Number of calves in group¶	−0.093	0.79	1	$P = 0.374$
Age of youngest calf in group	0.0148	1.11	1	$P = 0.291$
Presence or absence of adult males	−0.246	0.37	1	$P = 0.543$

*Deviances reported are those obtained when significant variables are dropped and when nonsignificant variables are added to the final model. †The final model explains a deviance of 56.8 out of a total deviance of 190.3. ‡Twenty-one families were fitted to the model as a factor, and hence coefficients for individual families are not reported. §All interactions between these variables and the age of the matriarch were not significant. ||The number and age of adult females present ("adult" defined by having reached the age of first conception: 11 years and over) were noted for every playback. ¶Calves were individuals of up to 3 years in age. **The final model explains a deviance of 10.7 out of a total deviance of 211.9.

Table 2. Regression analysis of factors affecting the reproductive success of elephant family units (calves per female reproductive year) over the course of our study.

Variable	Coefficient	t	df	Significance
Reproductive success*				
Age of matriarch	0.0011	3.01	18	$P = 0.008$
Mean number of females in group	−0.0025	−2.13	18	$P = 0.048$
Residual reproductive success†				
Point of inflection on bunch analysis‡	27.1	1.86	14§	$P = 0.084¶$
Point of inflection on smell analysis	21.0	2.06	17	$P = 0.055¶$

*The model explains 30.7% of a total variance of 0.0088. Data were log-transformed before analysis to conform to a normal distribution. †The inflection points for bunching and smelling were entered separately in these analyses. ‡The model explains 12.6% of a total variance of 17.92. §The logistical curves were flat for three families, and hence inflection points could not be calculated, thus reducing degrees of freedom. ¶The model explains 14.0% of a total variance of 22.20. ¶Indicative of significance.

fects on the acquisition of social knowledge and that the possession of enhanced discriminatory abilities by the oldest individual in a group of advanced social mammals can influence the social knowledge of the group as a whole. These findings have important implications for conservation as well as evolutionary biology. Tusk size in elephants is related to age, and hunters focus their efforts on individuals that have large tusks (21). In view of our results, it is clear that the removal of matriarchs from elephant family units could have serious consequences for the conservation of this endangered species. Indeed, in many mammal societies, the oldest individuals are also the largest, and these tend to be particular targets of hunters (22) and poachers. If groups rely on older members for their store of social knowledge, then whole populations may be affected by the removal of a few key individuals.

References and Notes

1. N. K. Humphrey, in *Growing Points in Ethology*, P. P. G. Bateson, R. A. Hinde, Eds. (Cambridge Univ. Press, Cambridge, 1976), pp. 303–317.
2. D. L. Cheney, R. M. Seyfarth, *How Monkeys See the World: Inside the Mind of Another Species* (Univ. of Chicago Press, Chicago, 1990).
3. R. I. M. Dunbar, *Behav. Brain Sci.* **16**, 681 (1993).
4. G. Gigerenzer, in *Machiavellian Intelligence II, Extensions and Evaluations*, A. Whiten, R. W. Byrne, Eds. (Cambridge Univ. Press, Cambridge, 1997), pp. 264–288.
5. R. C. Connor, in *Cetacean Societies, Field Studies of Dolphins and Whales*, J. Mann, R. C. Connor, P. L. Tyack, H. Whitehead, Eds. (Univ. of Chicago Press, Chicago, 2000), pp. 199–218.
6. T. Nishida, M. Hiraiwa-Hasegawa, in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (Univ. of Chicago Press, Chicago, 1986), pp. 165–177.
7. C. J. Moss, J. H. Poole, in *Primate Social Relationships: An Integrated Approach*, R. A. Hinde, Ed. (Blackwell Scientific, Oxford, 1983), pp. 315–325.
8. Families were considered to encounter another family during the year if they were sighted at least once within the same group. We calculated the number of families encountered per year by each of the 21 families of subjects that were part of the current study for the years of the study (from January 1993 to December 1999). On this basis, the mean number of families encountered per year was 24.8, with a standard error of 1.35.
9. K. McComb, C. Moss, S. Sayialel, L. Baker, *Anim. Behav.* **59**, 1103 (2000).
10. C. Moss, in *Studying Elephants*, K. Kangwana, Ed. (African Wildlife Foundation, Nairobi, Kenya, 1996), pp. 58–74.
11. Contact calls recorded from a total of 20 adult females, all known individuals in the study population, were used as playback stimuli. All recordings were made on digital audio tape using equipment specialized for low-frequency recording: a Sennheiser MKH 110 microphone linked to a Sony TCD D10 DAT recorder (with DC modification) or a HHB PortaDAT PDR 1000 DAT recorder. The system for playback was composed of a custom-built 6th-order bass box loudspeaker (Aylestone, Cambridge, UK) with two sound ports linked to a power amplifier [a Kenwood KAC-PS400M or amplifiers described in (9)], which had a lower frequency limit of 10 Hz and a response that was flat $\pm$ 4 dB from $\sim$ 15 Hz on one sound port and $\sim$ 20 Hz on the other. Each of 21 families of subjects received playbacks of contact calls from a mean of 8 different callers (range: 4 to 11), none of which were members of their own family unit or bond group. Calls were only played if the subjects were within their home range and had no calves of less than 1 month. Playbacks to the same family unit were always separated by at least 7 days, and playbacks of callers of different association indices with the subjects were given in random order. In each playback, a single contact call was played at peak sound pressure levels of 105 dB at 1 m (corresponding to the natural volume of a medium loud contact call) from a Landrover vehicle that was located 100 m from the subjects. The vehicle was positioned at right angles to the direct line of sight to the elephants, and vocalizations were played through the rear door. Responses to playbacks were observed through binoculars and recorded on videotape. Out of a range of behaviors monitored during playback experiments, two key behaviors were used to classify subjects' reactions in this study: (i) Bunching: scored as occurring if subjects bunched together into defensive formation so that the diameter (estimated in terms of elephant body lengths) of the whole group, or of constituent subgroups, decreased. (ii) Smelling: scored as occurring when any of the subjects used the tip of their trunk to smell, in lowered, mid-, or raised positions.
12. Data on the ranging and association patterns of female study animals were obtained from regular monitoring of elephant family units. Association indices were calculated for the period from January 1993 to December 1999 as $NAB/(NA + NB + NAB)$, where NAB = number of times families A and B are sighted in association in the same group; NA = number of times family A is sighted without B; and NB = number of times family B is sighted without A. This "same-group" measure of association is more restrictive than that used in our previous study (9). The association indices for the 21 families in our study were based on a total of 6685 sightings of these families.
13. J. H. Poole, K. Payne, W. R. Langbauer, C. J. Moss, *Behav. Ecol. Sociobiol.* **22**, 385 (1988).
14. All statistical analyses were carried out with Genstat [R. W. Payne et al., *GENSTAT 5 Reference Manual* (Oxford Univ. Press, Oxford, 1987)].
15. Ages were known for elephants born after 1971, and ages for older individuals were estimated on the basis of well-defined criteria that are accepted as a standard in studies of African elephants (10).
16. C. A. Spina, *Elephants* (T & A D Poyser, London, 1994).
17. We used the number of calves produced per female reproductive year as a standardized measure of reproductive success over the years of our study (from January 1993 to December 1999). This measure controls for the number of reproductive years available to females of different ages in the family. For each family, the total number of calves surviving to at least 1 year over that period was calculated and was divided by the total number of reproductive years that females in the family potentially had to reproduce, assigning females a reproductive year for every year that they were reproductively viable: at least 13 years old (the age of first birth) but less than 60 years old (the age of last birth).
18. K. J. McConway, M. C. Jones, P. C. Taylor, *Statistical Modelling Using Genstat* (Arnold (in association with the Open University), London, 1999).
19. N. Ratcliffe, R. W. Furness, K. C. Hamer, *J. Anim. Ecol.* **67**, 853 (1998).
20. S. M. Durant, *Anim. Behav.* **60**, 121 (2000).
21. A. Dobson, J. Poole, in *Behavioural Ecology and Conservation Biology*, T. M. Caro, Ed. (Oxford Univ. Press, Oxford, 1998), pp. 193–208.
22. P. T. Stevick, *Mar. Mamm. Sci.* **15**, 725 (1999).
23. We thank the Biotechnology and Biological Sciences Research Council for providing the major funding for this work (grant no. 85/S07659 to K.M.). Additional financial support or equipment came from the African Wildlife Foundation; the Association for the Study of Animal Behaviour; Newnham College (Cambridge); the Natural Environment Research Council; the Nuffield Foundation; the Royal Society; the Tusk Trust; the University of Sussex; and the Institute of Zoology. We are grateful to the Kenyan Office of the President and to Kenya Wildlife Services for permission to conduct the work in Amboseli National Park; to the African Wildlife Foundation and P. B. Allen for logistical support; to K. Sayialel and N. Njiriana for assistance with fieldwork; and to P. Harvey, G. Mace, and D. Reby for comments on the manuscript.

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Fecundity-Survival Trade-Offs and Parental Risk-Taking in Birds

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Life history theory predicts that parents should value their own survival over that of their offspring in species with a higher probability of adult survival and fewer offspring. We report that Southern Hemisphere birds have higher adult survival and smaller clutch sizes than Northern Hemisphere birds. We subsequently manipulated predation risk to adults versus offspring in 10 species that were paired between North and South America on the basis of phylogeny and ecology. As predicted, southern parents responded more strongly to reduce mortality risk to themselves even at a cost to their offspring, whereas northern parents responded more strongly to reduce risk to their offspring even at greater risk to themselves.

Should parents place themselves, or their offspring, at greater risk of mortality when threatened with predation? Theoretical models of life history evolution predict that the resolution to this dilemma will vary among species depending on offspring number and the probability of survival for the parents (1–5). Parents should tolerate greater risk to

themselves, but not their young, in species with many offspring and reduced adult survival because the fitness value of the current brood is high and the probability of surviving to breed in the future is low (i.e., residual reproductive value is low). In contrast, parents of species with fewer offspring and higher probability of adult survival should tolerate