creased proliferation, growth, and survival by means other than *Ras^{V12}* are not sufficient to cause the metastatic progression of *scrib^{–/–}* cells. Thus, the metastasis-promoting effect of *scrib* inactivation is highly dependent on its specific cooperation with the *Ras^{V12}* allele. Moreover, aside from its known effects on proliferation, growth, and survival, *Ras^{V12}* may function through an as yet undefined cellular mechanism to elicit metastatic progression in *scrib^{–/–}* cells.

It has proven difficult to systematically study the genetic basis of metastasis with the currently available techniques. The *Drosophila* system described here circumvents the complication of acquired background mutations, which can occur through repeated passaging of cell lines or during the typically long latent period of mammalian tumor progression. In our initial screen, we found that mutations in different genes affecting the same physiological process—epithelial cell polarity maintenance—are sufficient in combination with *Ras^{V12}* to promote metastatic behavior in vivo. Interestingly, later stage human cancers typically lose cell polarity markers and epithelial structure during epithelial to mesenchymal transition (*31*). Also, E-cadherin loss, basement membrane degradation, and induction of cell migration and invasion relate well to observations made in human metastasis (*15, 31, 32*), which suggests that the ongoing screen will uncover genes and general mechanisms relevant to malignancy in humans.

It has been proposed that oncogenes such as *Ras* may play a dual role in tumorigenesis and metastasis (*33*); however, this has not yet been rigorously proven in mammalian systems, as the effects of *Ras* in cell culture depend greatly on the particular cell line used. We provide experimental evidence that genetic alterations promoting noninvasive tumor growth can indeed make additional contributions to the development of metastatic behavior, as *Ras^{V12}* expression is a crucial factor in making cell polarity–deficient cells metastasize. Furthermore, we show that oncogenic *Ras* specifically cooperates with inactivation of cell polarity genes to promote metastatic behavior. This may provide an explanation for the different metastatic potential observed in tumors of distinctive origins. The *Drosophila* genetics techniques described here should make it easier to analyze the specific targets of *Ras^{V12}* in metastatic cells, to identify other genes that cooperate with *Ras^{V12}* or other oncogenic alterations in promoting metastasis, and to elucidate the cellular processes that go awry during metastatic progression.

References and Notes

1. A. F. Chambers, A. C. Groom, I. C. MacDonald, *Nature Rev. Cancer* **2**, 563 (2002).
2. P. S. Steeg, *Nature Rev. Cancer* **3**, 55 (2003).
3. C. J. Potter, G. S. Turenchalk, T. Xu, *Trends Genet.* **16**, 33 (2000).
4. R. A. Pagliarini, A. T. Quinones, T. Xu, in *Tumor Suppressor Genes: Regulation, Function, and Medici-*
nal Applications, W. S. El-Deiry, Ed. (Humana, Totowa, NJ, 2003), pp. 349–381.
5. See supporting material on *Science* Online.
6. T. P. Newsome, B. Asling, B. J. Dickson, *Development* **127**, 851 (2000).
7. *ey* also expresses in the CNS, ocelli, and Bolwig's organ. In larvae, however, *eyFLP* did not produce visible clones outside of the noted locations.
8. M. A. St. John *et al.*, *Nature Genet.* **21**, 182 (1999).
9. F. D. Karim, G. M. Rubin, *Development* **125**, 1 (1998).
10. G. H. Fisher *et al.*, *Genes Dev.* **15**, 3249 (2001).
11. T. Xu, W. Wang, S. Zhang, R. A. Stewart, W. Yu, *Development* **121**, 1053 (1995).
12. Three phenotypic classes were observed when *Ras^{V12}*-expressing cells in mosaic flies were also made homozygous for additional second-site mutations (862 mutant lines): reduced tumor growth (76 lines), enhanced tumor growth (9 lines), and tumors with metastatic behavior (2 lines).
13. D. Bilder, N. Perrimon, *Nature* **403**, 676 (2000).
14. D. Bilder, M. Li, N. Perrimon, *Science* **289**, 113 (2000).
15. M. Egeblad, Z. Werb, *Nature Rev. Cancer* **2**, 161 (2002).
16. X. Morin, R. Daneman, M. Zavortink, W. Chia, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 15050 (2001).
17. When using the GFP-labeled collagen IV protein trap, mutant cells were marked with *UAS-lacZ* instead of *UAS-GFP*.
18. A. K. Perl, P. Wilgenbus, U. Dahl, H. Semb, G. Christofori, *Nature* **392**, 190 (1998).
19. T. Uemura *et al.*, *Genes Dev.* **10**, 659 (1996).
20. U. Tepass *et al.*, *Genes Dev.* **10**, 672 (1996).
21. J. L. Genova, S. Jong, J. T. Camp, R. G. Fehon, *Dev. Biol.* **221**, 181 (2000).
22. H. A. Muller, E. Wieschaus, *J. Cell Biol.* **134**, 149 (1996).
23. D. Bilder, M. Schober, N. Perrimon, *Nature Cell Biol.* **5**, 53 (2003).
24. G. Tanentzapf, U. Tepass, *Nature Cell Biol.* **5**, 46 (2003).
25. A. Bergmann, J. Agapite, K. McCall, H. Steller, *Cell* **95**, 331 (1998).
26. D. A. Prober, B. A. Edgar, *Cell* **100**, 435 (2000).
27. W. Du, J. E. Xie, N. Dyson, *EMBO J.* **15**, 3684 (1996).
28. B. A. Hay, T. Wolff, G. M. Rubin, *Development* **120**, 2121 (1994).
29. L. A. Johnston, D. A. Prober, B. A. Edgar, R. N. Eisenman, P. Gallant, *Cell* **98**, 779 (1999).
30. J. Verdu, M. A. Buratovich, E. L. Wilder, M. J. Birnbaum, *Nature Cell Biol.* **1**, 500 (1999).
31. J. P. Thiery, *Nature Rev. Cancer* **2**, 442 (2002).
32. P. Guilford, *Mol. Med. Today* **5**, 172 (1999).
33. R. Bernards, R. A. Weinberg, *Nature* **418**, 823 (2002).
34. T. Xu, G. M. Rubin, *Development* **117**, 1223 (1993).
35. T. Lee, L. Luo, *Neuron* **22**, 451 (1999).
36. K. Ito, W. Awano, K. Suzuki, Y. Hiromi, D. Yamamoto, *Development* **124**, 761 (1997).
37. A. H. Brand, N. Perrimon, *Development* **118**, 401 (1993).
38. M. Therrien, A. M. Wong, G. M. Rubin, *Cell* **95**, 343 (1998).
39. We thank D. DiMaio, A. Horwich, R. Lifton, D. Stern, and K. White for critical review; R. Li, T. Ni, and H. Lee for participating in the screen; X. Fei for transgene injections; E. Hersperger and A. Shearn for teaching transplantation techniques; and D. Bilder, M. Birnbaum, H. Chang, L. Cooley, R. Fehon, P. Gallant, I. Hariharan, B. Hay, X. Morin, H. Oda, J. P. Vincent, and T. Uemura for strains and reagents. Supported by NIH grant CA69408 (T.X.) and the Linda Tallen and David Paul Kane Educational and Research Foundation. T.X. is a HHMI Investigator; R.A.P. is a predoctoral fellow in the Department of Genetics.

Social Bonds of Female Baboons Enhance Infant Survival

Joan B. Silk,[1]* Susan C. Alberts,[2,4] Jeanne Altmann[3,4,5]

Among nonhuman primates, females often form strong bonds with kin and other group members. These relationships are thought to have adaptive value for females, but direct effects of sociality on fitness have never been demonstrated. We present 16 years of behavioral data from a well-studied population of wild baboons, which demonstrate that sociality of adult females is positively associated with infant survival, an important component of variation in female lifetime fitness. The effects of sociality on infant survival are independent of the effects of dominance rank, group membership, and environmental conditions. Our results are consistent with the evidence that social support has beneficial effects on human health and well-being across the life span. For humans and other primates, sociality has adaptive value.

Social relationships play an important role in the daily lives of females in many species of nonhuman primates. In some species, females form close and enduring relationships with other group members, and they spend a substantial amount of time grooming and resting together (*1*). These social bonds have long been presumed to have adaptive consequences for females (*2*), but there has been no evidence directly linking the quality of social bonds to fitness outcomes. Here, we present evidence for such effects, supporting the hypothesis that social bonds have adaptive value for primates.

We draw on data from a long-term study of wild savannah baboons, *Papio cynocephalus*, in the Amboseli basin of Kenya to examine the relationship between social inte-

[1]Department of Anthropology, University of California, Los Angeles (UCLA), CA 90095, USA. [2]Department of Biology, Duke University, Durham, NC 27708, USA. [3]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. [4]Institute for Primate Research, National Museums of Kenya, Nairobi, Kenya. [5]Department of Conservation Biology, Brookfield Zoo, Brookfield, IL 60513, USA.

*To whom correspondence should be addressed. E-mail: jsilk@anthro.ucla.edu

gration and female reproductive performance. Savannah baboons are an appropriate subject for this kind of analysis because they are highly gregarious and live in large mixed-sex groups. Females remain in their natal groups throughout their lives, whereas males disperse from their natal groups when they mature (*3*). Females form stable matrilineal dominance hierarchies in which maternal kin occupy adjacent ranks (*3*). Females establish strong and well-differentiated relationships with other adult females in their groups (*4*). Female-female relationships are typically characterized by frequent grooming, close spatial proximity, and occasional acts of coalitionary support (*4*, *5*). Social relationships among females are hypothesized to be valuable to adult females because they enhance the prospects of obtaining coalitionary support in within-group contests (*6*) or increase tolerance from more powerful group members (*7*). Social relationships among females may also provide a benign environment for raising and socializing their offspring. Social relationships with adult males may be valuable to females because male associates shield females from harassment (*8*), support their offspring in agonistic interactions (*9*), and in some populations protect the females' infants from predators or infanticidal attacks (*10*).

We studied the members of several well-habituated baboon groups that occupied overlapping home ranges in the Amboseli basin at the foot of Mount Kilimanjaro (*11*). The study population is derived from two groups, Alto's Group and Hook's Group, which have been monitored continually since 1971 and 1980, respectively. During the study period (1984 to 1999), both of the original study groups shifted their home ranges and fissioned (*11*, *12*).

Behavioral data were derived from 10-min focal samples of adult females (*11*). Data on reproductive events and infant survival were derived from demographic records that contain information about all pregnancies, births, deaths, and maturational events. Monthly dominance ranks for adult females were computed from the outcome of dyadic agonistic encounters observed during focal samples and ad libitum (*11*). The analyses described in this report are based on about 34,000 focal samples of 108 adult females during 633 female years.

We calculated infant survival for each female as the proportion of infants that survived to 1 year of age, the major period of infant dependency in this species. We focused on survival to 1 year because infant survival is a major component of fitness for any organism, and it has particularly large effects on long-lived animals that reproduce slowly (*13*). Further, both empirical and modeling results for the Amboseli baboons indi-

cate that infant survival is an important source of variation in lifetime fitness among females, arguably the most important one (*14*). For each female, we computed the difference between the proportion of infants that survived to 1 year and the median proportion of all infants born in the population that survived to 1 year of age. High values of this measure, labeled relative infant survival, represent females who reproduced more successfully than the median female, and low values represent females who reproduced less successfully than the median female.

Our focal samples yielded three measures of sociality, each of which is a probability estimate based on the proportion of point samples (i) in which an adult conspecific is with 5 m, (ii) being groomed by other adults, and (iii) grooming other adults. Grooming and maintaining proximity to other group members represent the major components of female baboons' social time and are widely considered to provide meaningful measures of social relationships among nonhuman primates (*15*). We combined these three measures into a single composite measure of sociality, the composite sociality index (*16*, *17*). We used this composite index, rather than investigating the three measures independently, because they were highly intercorrelated (proximity × grooming others: Spearman rank correlation test $r_s = 0.439$, $P < 0.001$; proximity × being groomed: $r_s = 0.303$, $P = 0.001$; grooming others × groomed: $r_s = 0.404$, $P < 0.001$; $N = 108$). Further, each was positively related to relative infant survival in linear regressions (*18*) with relative infant survival as the response variable, although not all were statistically significant predictors on their own (predictor variables were proximity: $\beta = 0.460$, $t = 1.85$, $P = 0.068$; being groomed: $\beta = 0.175$, $t = 3.28$, $P = 0.001$; and grooming others: $\beta = 0.095$, $t = 1.42$, $P = 0.159$; $N = 108$).

The composite sociality index provides a measure of the extent to which each female deviates from the global population on all three measures combined; high composite sociality index values represent females who were more socially integrated than the median female, and low composite sociality index values represent females who were less socially integrated than the median female.

The social integration of females was a significant predictor of infant survival (Fig. 1). Females who had high composite sociality index scores had offspring with relatively higher survival than females who had low composite sociality index scores (Table 1). High dominance rank is associated with high values of both the composite sociality index and relative infant survival (Table 1), raising the possibility that the relationship between the composite sociality index and relative infant survival is an artifact of variation in

female dominance rank. However, the relationship between sociality and infant survival remains significant when the effects of dominance rank are accounted for statistically in a multiple regression (Table 1).

Sociality and infant survival varied considerably over the study period, and this is likely to be linked to temporal changes in environmental conditions over the course of the study and to changes in habitat quality associated with the groups' home range shifts (*12*, *14*, *19*). Females who were observed in more favorable habitats or during more favorable time periods might have been more social and reproduced more successfully than females observed during less favorable periods, raising the possibility that the relationship between sociality and infant survival is an artifact of variation in habitat quality. To control for this possibility, we adjusted our measures of sociality and infant survival (*20*). We did not assess environmental conditions directly, but we controlled for the effects of ecological variation by comparing each female to other females living in the same group at the same time in the same habitat. High values of the adjusted composite sociality index represent females who were more socially integrated than other females living in the same group at the same time in the same habitat, and high values of adjusted relative infant survival represent females who reproduced more successfully than other females who were living in the same group at the same time in the same habitat.

As before, we found that females who were more fully socially integrated (defined by higher adjusted composite social-
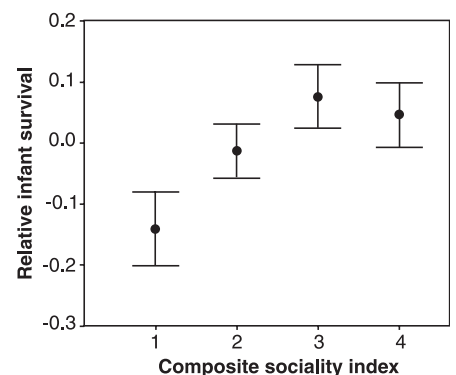

Fig. 1. Effects of sociality on infant survival. For the purposes of visual representation, composite sociality index scores were ranked from low to high, and divided into four quartiles [statistical analyses were performed on composite sociality index scores as a continuous variable (Table 1)]. Quartile 1 includes the females with the lowest composite sociality index scores, and quartile 4 includes females with the highest composite sociality index scores. Means and standard errors of the mean of relative infant survival for each quartile are shown. For each quartile, $N = 27$.

ity index values) had higher adjusted relative infant survival among their offspring (Table 1). This result remains significant when the effects of dominance rank are accounted for statistically in a multiple regression (Table 1).

Our data indicate that social integration has positive effects on the reproductive performance of female baboons. Females who had more social contact with other adult group members and were more fully socially integrated into their groups were more likely than other females to rear infants successfully. These effects were independent of female dominance rank and variation in ecological conditions that affected both females' behavior and their reproductive performance. Thus, these data provide direct empirical evidence that sociality enhances the fitness of nonhuman primate females.

Our findings are consistent with data derived from epidemiological and clinical studies of humans. Social support has beneficial effects on health and well-being across the life span (21–24). Social isolation increases the risk of disease, accidents, and a range of mental disorders, and the disruption of social ties, due to death, divorce, or separation, is a major source of stress. Feelings of loneliness are associated with psychological disturbances, and loneliness increases morbidity and mortality (25). Among low-income women, those with more extensive social networks give birth to heavier infants (26). Experimental studies in humans suggest that social integration is the cause not the consequence of improved health outcomes. Social support is thought to moderate the deleterious effects of chronic stress and thereby enhance well-being.

Social contact seems to have similar kinds of effects in other species (27). Human handling reduces cardiovascular responses to stressors in dogs, cats, horses, and rabbits (21). In the laboratory, group-living delays reproductive senescence in female rats (28) and enhances longevity (22). The presence of familiar conspecifics buffers experimentally induced stress in rats, mice, goats, and monkeys (21, 27). Basal cortisol levels decline when squirrel monkey females are housed with conspecific partners (29), and social isolation exacerbates coronary artery atherosclerosis among female long-tailed macaques (30). Captive long-tailed macaques tend to affiliate at higher rates when social conditions are unstable, and this is associated with enhanced immune responsiveness (31). In the Amboseli baboon population, social integration is linked to reduced levels of basal cortisol among adult males (17).

It is not yet clear whether the mechanisms that underlie the relationship between sociality and infant survival in baboons are the same as the mechanisms that link social contact and health outcomes in humans. Close association with other group members may ameliorate the deleterious effects of stress in nonhuman primates in much the same way as it does in humans. For example, grooming reduces heart rate in some monkey species, and may induce release of β-endorphins (32). Similarly, heart rate and the rate of self-directed behaviors that are correlated with physiological measures of stress decline when females reconcile with former opponents (32). Alternatively, close association with other group members may provide females and their dependent offspring with direct material benefits, such as protection from harassment or access to valuable resources. For example, in Amboseli, adult females spend much of their time near their kin, who are also their most frequent allies in agonistic disputes (5). Female baboons also spend time near adult males who sometimes protect them and their offspring from harassment (8–10). All of these factors, and others that we have not yet considered, may contribute to the relationship between sociality and infant survival. Whatever the mechanism, our data demonstrate that social relationships have adaptive value for primate females.

References and Notes

1. R. I. M. Dunbar, *Folia Primatol.* **57**, 121 (1991).
2. D. L. Cheney, R. M. Seyfarth, B. B. Smuts, *Science* **234**, 1361 (1986).
3. D. J. Melnick, M. C. Pearl, in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (Univ. Chicago Press, Chicago, IL, 1987), pp. 121–134.
4. J. B Silk, R. M. Seyfarth, D. L. Cheney, *Behaviour* **136**, 679 (1999).
5. J. B. Silk, S. C. Alberts, J. Altmann, *Anim. Behav.*, in press.
6. E. H. M. Sterck, D. P. Watts, C. P. van Schaik, *Behav. Ecol. Sociobiol.* **41**, 291 (1997).
7. S. P. Henzi, L. Barrett, *Primates* **40**, 47 (1999).
8. B. B. Smuts, *Sex and Friendship in Baboons* (Aldine, New York, 1985).
9. J. Buchan, S. C. Alberts, J. B. Silk, J. Altmann, *Nature* **425**, 179 (2003).
10. R. A. Palombit, *Evol. Anthropol.* **7**, 117 (1999).
11. Additional information about the study population, data collection protocol, and analysis is available as supporting material on *Science* Online.
12. S. C. Alberts *et al.*, in *Primate Seasonality: Implications for Human Evolution*, D. K. Brockman, C. P. van Schaik, Eds. (Cambridge Univ. Press, Cambridge, in press).
13. T. H. Clutton-Brock, in *Reproductive Success*, T. H. Clutton-Brock, Ed. (Univ. Chicago Press, Chicago, IL, 1988), pp. 472–485.
14. J. Altmann, S. C. Alberts, in *Offspring: Human Fertility Behavior in Biodemographic Perspective*, K. W. Wachter, R. A. Bulatao, Eds. (National Academies Press, Washington, DC, 2003), pp. 140–169.
15. M. Cords, in *Machiavellian Intelligence II*, A. Whiten, R. W. Byrne, Eds. (Cambridge Univ. Press, Cambridge, 1997), pp. 24–49.
16. We computed a composite index of social integration for each female as follows:

$$\frac{\sum\limits_{i=1}^{3} \dfrac{x_i}{m_i}}{3}$$

where the values of x_i are those for each of the three behavioral measures for the female, and the values of m_i are the median values of the respective behavioral measure for the population. A similar index was originally used by Sapolsky, Alberts, and Altmann (17).
17. R. M. Sapolsky, S. C. Alberts, J. Altmann, *Arch. Gen. Psychiatry* **54**, 1137 (1997).
18. To assess the bivariate relationships among the behavioral variables (proximity, grooming others, and being groomed) we used Spearman's nonparametric rank correlations. To measure the extent to which each of these behaviors predicted relative infant survival, and then to measure the extent to which the composite sociality index and dominance rank predicted relative infant survival, we used regression with robust standard errors (33). This regression technique is appropriate when residuals are non-normal or when there is heteroskedasticity in the residuals. All statistical analyses were conducted with STATA 8.0 (34).
19. A. Bronikowski, J. Altmann, *Behav. Ecol. Sociobiol.* **39**, 11 (1996).
20. To control for the effects of ecological conditions, we compared females to other females living in the same groups in the same habitat at the same time. For Alto's Group, which was studied for 4 years before the move and 11 years after the move, we divided

Table 1. Predictors of relative infant survival (RIS) and adjusted relative infant survival (adj. RIS). Regression with robust standard errors (18, 33) was used to measure the extent to which sociality and dominance rank predicted infant survival. CSI, composite sociality index; adj. CSI, adjusted values of composite sociality index. For the multivariate regressions, we report the partial-regression coefficients and parameters as well as the whole-model results. High-ranking females are assigned the lowest rank numbers, so negative coefficients indicate that higher ranking females had higher reproductive success than lower ranking females. The sample size for the regressions based on unadjusted values is 108; the sample size for the regressions based on adjusted values is 106, because two females who did not give birth during the study period were deleted from this portion of the analysis.

Model	Response variable	Predictor variables	Partial regression parameters	β	R^2	F	P	t
Bivariate	RIS	CSI		0.270	0.078	8.15	0.005	
Bivariate	RIS	Rank		−0.011	0.040	4.62	0.034	
Multivariate	RIS	CSI and rank			0.093	5.43	0.006	
			CSI	0.234			0.026	2.27
			Rank	−0.007			0.202	−1.28
Bivariate	Adj. RIS	Adj. CSI		0.332	0.081	7.20	0.009	
Bivariate	Adj. RIS	Rank		−0.007	0.011	1.21	0.275	
Multivariate	Adj. RIS	Adj. CSI and rank			0.082	3.67	0.029	
			Adj. CSI	0.321			0.015	2.48
			Rank	−0.002			0.685	−0.41

the study period into one "premove" and two "postmove" periods. For Hook's Group, which was observed for 9 years before the move and 7 years after the move, we divided the study period into two premove and one postmove periods. We calculated the value of the composite sociality index for each female during each time period using the median values of the three behavioral measures derived from each time period for each group. We computed the adjusted value of relative infant survival as the difference between the proportion of infants born to female x in group y in period z that survived to 1 year of age and the proportion of all infants born to all females in group y in period z that survived to 1 year. For females observed in multiple time periods, we based analyses on the mean of the adjusted values of the composite sociality index and adjusted relative infant survival across time periods. This procedure ensures that each data point is independent. Analyses based on the full data set generate very similar results.

21. J. S. House, K. R. Landis, D. Umberson, *Science* **241**, 540 (1988).
22. S. E. Taylor *et al.*, *Psychol. Rev.* **197**, 411 (2000).
23. T. E. Seeman, B. H. Singer, C. D. Ryff, G. D. Love, L. Levy-Storms, *Psychosomatic Med.* **64**, 395 (2002).
24. W. L. Gardner, S. Gabriel, A. B. Diekman, in *Handbook of Psychophysiology*, J. T. Cacioppo, L. G. Tassinary, G. G. Berntson, Eds. (Cambridge Univ. Press, New York, 2000), pp. 643–664.
25. J. T. Cacioppo *et al.*, *Int. J. Psychophysiol.* **35**, 143 (2000).
26. N. L. Collins, C. Dunkel-Schetter, M. Lobel, S. C. Scrimshaw, *J. Pers. Soc. Psychol.* **65**, 1243 (1993).
27. T. E. Seeman, B. S. McEwen, *Psychosomatic Med.* **58**, 459 (1996).
28. J. A. LeFevre, M. K. McClintock, *Physiol. Behav.* **52**, 603 (1992).
29. W. Saltzman, S. P. Mendoza, W. A. Mason, *Physiol. Behav.* **50**, 271 (1991).
30. C. A. Shively, T. B. Clarkson, J. R. Kaplan, *Atherosclerosis* **77**, 69 (1989).
31. S. Cohen, J. R. Kaplan, J. E. Cunnick, S. B. Manuck, B. S. Rabin, *Psychol. Sci.* **3**, 301 (1992).
32. F. Aureli, D. A. Smucny, in *Natural Conflict Resolution*, F. Aureli, F. B. M. de Waal, Eds. (Univ. California Press, Berkeley, CA, 2000), pp. 193–224.
33. H. White, *Econometrica* **48**, 817 (1980).
34. STATA 8.0, Stata, College Station, TX (2003).
35. We thank the Office of the President of Kenya and the Kenya Wildlife Service for permission to work in Amboseli; the staffs of the National Museums of Kenya, the Kenya Wildlife Service, and Amboseli National Park for cooperation and assistance; the members of the pastoralist communities of Amboseli and Longido and the Institute for Primate Research in Nairobi for assistance and local sponsorship; R. Mututua, S. Sayialel, P. Muruthi, and K. Warutere for their assistance with data collection; and D. Onderdonk for database assistance. Supported by grants from the National Geographic Society, the Louis S. B. Leakey Foundation, the UCLA Academic Senate, and NSF (to J.B.S.); the Chicago Zoological Society and NSF (to J.A.); and NSF (to S.C.A.).

Hierarchical Classification by Rank and Kinship in Baboons

Thore J. Bergman,[1]* Jacinta C. Beehner,[1] Dorothy L. Cheney,[1] Robert M. Seyfarth[2]

Humans routinely classify others according to both their individual attributes, such as social status or wealth, and membership in higher order groups, such as families or castes. They also recognize that people's individual attributes may be influenced and regulated by their group affiliations. It is not known whether such rule-governed, hierarchical classifications are specific to humans or might also occur in nonlinguistic species. Here we show that baboons recognize that a dominance hierarchy can be subdivided into family groups. In playback experiments, baboons respond more strongly to call sequences mimicking dominance rank reversals between families than within families, indicating that they classify others simultaneously according to both individual rank and kinship. The selective pressures imposed by complex societies may therefore have favored cognitive skills that constitute an evolutionary precursor to some components of human cognition.

Although nonhuman primates recognize other individuals' dominance ranks and kin relations (*1–8*), it is not known whether they classify others according to both criteria simultaneously. Humans make such higher order classifications routinely, and as a result easily recognize that not all superficially similar interactions have equal importance. For example, in Shakespeare's *Romeo and Juliet*, we discount Mercutio's teasing of Romeo as trivial because both Mercutio and Romeo are allied with the house of Montague. When Mercutio aims his taunts at Tybalt, however, we regard his behavior as more ominous because Tybalt is a Capulet. Our responses are guided in part by our tendency to organize social relations into a hierarchical structure, such as familial affiliation, that is governed by a functional set of rules: Quarrels

between families are potentially much more destructive than quarrels within families.

Social groups of Old World monkeys such as baboons, macaques, and vervets are composed of a number of different matrilines arranged in a stable, linear dominance hierarchy in which all female members of one matriline outrank or are outranked by all female members of another (*9–13*). Threats and supplants (interactions in which one animal retreats from the approach of another) are almost without exception directed by higher ranking individuals toward lower ranking individuals, and alliances usually target subordinate opponents (*14, 15*). Affinitive social behavior such as grooming is directed preferentially toward close matrilineal kin. Members of the same matrilineal kin group occupy adjacent ranks and usually retain the same relative ranks throughout their lives. Both within- and between-family rank reversals are rare. When within-family rank reversals do occur, however, they typically involve only two individuals and have little effect on

social relations outside the matriline. In contrast, occasional between-family rank reversals represent major social upheavals in which all the members of two or even more matrilines may lose or gain rank (*1, 16–18*). They therefore have the potential to influence the rank relations of many individuals.

Matrilineal kin groups and linear dominance rank orders are evident not only to human observers but also to the monkeys themselves. Both observations and playback experiments have demonstrated that monkeys recognize the matrilineal kin (or close associates) of other group members (*1, 5–8*). Similarly, monkeys appear not only to understand who is dominant or subordinate to themselves but also to recognize the relative dominance ranks of others (*1–4*). It remains unclear, however, whether monkeys are capable of evaluating other individuals simultaneously according to both rank and kinship or whether they can combine their knowledge of rank and kinship to recognize that some rank reversals have potentially much greater social importance than others.

To investigate this question, we designed a playback experiment in which free-ranging female baboons (*Papio hamadryas ursinus*) were played a sequence of calls mimicking a fight between two other females (*19*). Call sequences consisted of a series of threat-grunts by one individual played in conjunction with the screams of another. Threat-grunts are tonal, multisyllable, staccato calls that are produced only when female baboons are threatening individuals who are subordinate to themselves, whereas screams are given only by animals who are being threatened by a more dominant individual. Numerous experiments and acoustical analyses have indicated that monkey vocalizations are individually distinctive and that subjects discriminate among the voices of matrilineal kin (*7, 20*).

Subjects were 19 adult female baboons (> 6 years old) living in the Okavango Delta

[1]Department of Biology, [2]Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, USA.

*To whom correspondence should be addressed. E-mail: thore@sas.upenn.edu