

the study period into one "premove" and two "post-move" 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. Diekmann, 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.).

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Hierarchical Classification by Rank and Kinship in Baboons

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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 matrilineal groups 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 matrilineal groups 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

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in Botswana. Matrilineal kinship for all natal animals was known. A matriline included all individuals to the level of first cousin. When constructing within-family rank reversal sequences, however, we chose signalers who were more closely related to each other (either sisters, mothers and daughters, or nieces and aunts). The experiments used a within-subject design. On separate days, the same subject heard one of three different call sequences: (i) an anomalous threat-grunt-scream sequence mimicking a within-family rank reversal (e.g., in a group where family A outranks family B, B outranks C, and so on, the subordinate female B_3 threat-grunts and the dominant B_1 screams), (ii) an anomalous sequence mimicking a between-family rank reversal (e.g., C_1 threat-grunts and B_3 screams), and (iii) a no-reversal control sequence consistent with the female dominance hierarchy. In some control sequences, the signalers were related to each other (e.g., B_1 threat-grunts and B_3 screams); in others, they were unrelated (e.g., B_3 threat-grunts and C_1 screams). Sequences were constructed from the vocalizations of 19 different females. All signalers were unrelated (i.e., from a different matriline) to the subject who heard their calls.

Previous experiments had shown that subjects respond more strongly (by looking toward the speaker for longer durations) to playback sequences that mimic interactions inconsistent with the current dominance hierarchy than to those consistent with it (2). We therefore predicted that subjects would respond more strongly to both of the rank reversal sequences than to the control sequences. We further predicted that, if baboons were simultaneously sensitive to both rank and kin relations, they should respond more strongly to sequences that simulated a between-family rank reversal than to sequences that mimicked a within-family rank reversal. A between-family rank reversal is potentially much more important than a within-family rank reversal because it signals a possible change in the dominance relations of two entire matriline. It therefore has the potential to affect the relative ranks of many individuals rather than just two.

One possible confounder arose because members of the same matriline occupy adjacent ranks, whereas members of different matriline are often more widely separated in rank. As a result, subjects might respond more strongly to a between-family rank reversal sequence simply because the reversal involved individuals of more disparate ranks. We controlled for rank distance by ensuring that a proportion of the within-family rank reversals involved signalers from large matriline who were separated by as many as seven ranks. Similarly, a proportion of the between-family rank re-

versals involved signalers who were adjacent in rank; that is, the lowest ranking female in one matriline and the highest ranking female in the next.

Overall, there was a significant difference in the duration of subjects' responses to the three call sequences (Fig. 1). Subjects looked toward the speaker for significantly longer durations when hearing sequences that mimicked a between-family rank reversal than when hearing both within-family rank reversal sequences and no-reversal control sequences. In contrast, although subjects on average looked longer at within-family rank reversal sequences than at control sequences, this difference was not significant (Fig. 1). Among control sequences, subjects looked as long at sequences that mimicked a within-family dispute as at those that mimicked a between-family dispute (mean duration of looking, within-family controls: $x = 1.4$ s, $SD = 1.7$; between-family controls: $x = 1.3$ s, $SD = 1.6$; Mann-Whitney U test, $N_1 = 6$, $N_2 = 13$, $U = 36.5$, $P > 0.25$).

Subjects' responses to apparent rank reversals were unrelated to the rank distance separating the two signalers. In both within- and between-family rank reversal sequences, subjects looked for equally long durations at apparent reversals involving closely ranked opponents as at those involving more distantly ranked opponents (Fig. 2). Another alternative explanation for the animals' responses might be the possible novelty of proximity between the

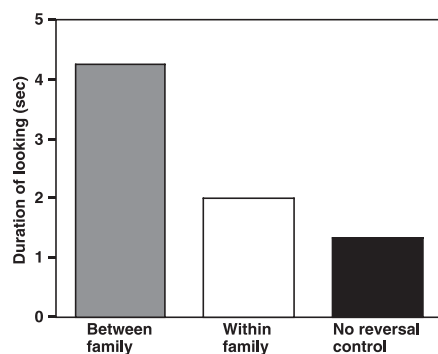


Fig. 1. The mean duration that subjects oriented toward the loudspeaker following playback of each sequence type. Overall, there was a significant difference in the duration of subjects' responses to the three call sequences (Friedman two-way analysis of variance, $df = 2$, $\chi^2 = 12.00$, $P < 0.01$). Subjects responded for significantly longer durations to between-family rank reversal (BFRR) sequences than to both within-family rank reversal (WFRR) sequences (Wilcoxon matched-pairs signed-rank test, $N = 18$, 2 ties, $T = 22.5$, $P < 0.01$) and control sequences ($N = 19$, 2 ties, $T = 20$, $P < 0.01$). There was no significant difference between the duration of subjects' responses to WFRR and control sequences ($N = 18$, 3 ties, $T = 47$, $P > 0.25$).

different matriline. However, females were more likely to have non-kin than kin as nearest neighbors (21). Finally, subjects' responses were not affected by the relative frequency of fights among kin as opposed to non-kin. Among kin dyads, aggressive interactions that included threat-grunts and screams occurred at an average rate of 5.4 times per 1000 hours of observation, compared with 6.5 times for non-kin dyads. In no case did these aggressive interactions involve threats or screams that violated the dominance hierarchy.

One explanation for subjects' relatively weak responses to within-family rank reversals is that they treated all members of the same matriline as effectively equivalent and therefore failed to distinguish among their ranks. According to this argument, kin were grouped into the same "equivalence class" as a result of their high rate of association, becoming both interchangeable and mutually substitutable (22). This argument has some validity. Indeed, the hypothesis that monkeys perceive within-family rank reversals as less important than between-family rank reversals assumes that members of the same matriline are classified into the same subgroup. This does not imply, however, that monkeys do not recognize the relative ranks of matrilineal kin. During this study, as in most other studies of Old World monkeys (1, 13, 16, 23), rates of aggression among members of the same matriline were similar to those among unrelated females, and their relative ranks were as stable as those of non-kin. Indeed, during the 10 years preceding these experiments, there were no changes in the adult female dominance hierarchy other than those caused by recruitment and mortality. There was therefore as much opportunity for baboons to learn the ranks of kin as of non-kin.

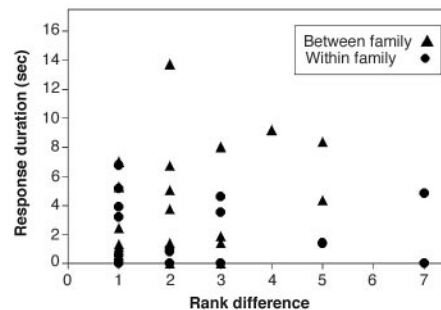


Fig. 2. The correlation between the strength of subjects' responses and the disparity in rank between the two signalers involved in the apparent rank reversal. Subjects did not respond for longer durations to sequences involving distantly ranked, as opposed to closely ranked, opponents (between-family rank reversal: Spearman rank correlation, $N = 19$, $r_s = 0.225$, $P > 0.25$; within-family rank reversal: $N = 18$, $r_s = -0.016$, $P > 0.25$).

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These experiments provide evidence that monkeys classify others simultaneously according to both their individual attributes and their membership in higher order groups, and that they do so in the absence of human training. Baboons appear to understand that their group's female dominance hierarchy can be subdivided into matriline. As a result, they may recognize that, although predictable rank relations are maintained both within and between matrilines, the latter are qualitatively different from the former.

These results may also be relevant to theories concerned with the evolution of human language. As many authors have noted, humans deduce the meaning of sentences by arranging words into nested, hierarchical groups that are defined according to their function as noun phrases, verb phrases, and so on (24, 25). At present, it is not known whether the formation of such rule-governed, hierarchical groups is specific to language or might have evolved to serve other, nonlinguistic purposes, for example in the domains of number, spatial memory, or social relations (26, 27). Our results suggest that baboons organize their companions into a hierarchical, rule-governed structure based simultaneously on kinship and rank. The se-

lective pressures imposed by life in complex social groups may therefore have favored cognitive skills that constitute an evolutionary precursor to at least some components of human behavior.

References and Notes

1. D. L. Cheney, R. M. Seyfarth, *How Monkeys See the World: Inside the Mind of Another Species* (Chicago Univ. Press, Chicago, 1990).
2. D. L. Cheney, R. M. Seyfarth, J. B. Silk, *J. Comp. Psych.* **109**, 134 (1995).
3. A. Sinha, *Phil. Trans. Roy. Soc. Lond. B* **353**, 619 (1998).
4. J. B. Silk, R. M. Seyfarth, D. L. Cheney, *Behaviour* **136**, 679 (1999).
5. V. Dasser, *Anim. Behav.* **36**, 225 (1988).
6. F. Aureli, R. Cozzolino, C. Cordischi, S. Scucchi, *Anim. Behav.* **44**, 283 (1992).
7. D. Rendall, P. S. Rodman, R. E. Emond, *Anim. Behav.* **51**, 1007 (1996).
8. D. L. Cheney, R. M. Seyfarth, *Anim. Behav.* **58**, 67 (1999).
9. S. Gouzoules, H. Gouzoules, in *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker, Eds. (Chicago Univ. Press, Chicago, 1987), pp. 299–305.
10. J. R. Walters, R. M. Seyfarth, in *Primate Societies*, B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker, Eds. (Chicago Univ. Press, Chicago, 1987), pp. 306–317.
11. G. Hausfater, J. Altmann, S. Altmann, *Science* **217**, 752 (1982).
12. J. B. Silk, *Anim. Behav.* **58**, 45 (1999).
13. J. B. Silk, *Int. J. Primatol.* **17**, 445 (2002).
14. B. Chapais, *Int. J. Primatol.* **22**, 203 (1991).
15. J. B. Silk, S. C. Alberts, J. Altmann, *Anim. Behav.*, in press.
16. A. Samuels, J. Silk, J. Altmann, *Anim. Behav.* **35**, 785 (1987).
17. B. Chapais, *Behaviour* **104**, 41 (1988).
18. C. Ehardt, I. Bernstein, *Int. J. Primatol.* **7**, 157 (1986).
19. Materials and methods are available as supporting material on Science Online.
20. R. M. Seyfarth, D. L. Cheney, *Ann. Rev. Psych.* **54**, 145 (2003).
21. T. J. Bergman, J. C. Beehner, unpublished data.
22. R. J. Schusterman, D. A. Kastak, *Anim. Behav.* **55**, 1087 (1988).
23. I. S. Bernstein, in *Kin Recognition*, P. G. Hepper, Ed. (Cambridge Univ. Press, Cambridge, 1991), pp. 6–29.
24. S. Pinker, *The Language Instinct* (Harper, New York, 1995).
25. R. Jackendoff, *Foundations of Language: Brain, Meaning, Grammar, Evolution* (Oxford Univ. Press, Oxford, 2002).
26. M. D. Hauser, N. Chomsky, W. T. Fitch, *Science* **298**, 1569 (2002).
27. T. Macuda, W. A. Roberts, *J. Exp. Psych. Anim. Behav. Proc.* **21**, 20 (1995).
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