

DOMINANCE RELATIONS AMONG FREE-RANGING FEMALE BABOONS
IN GOMBE NATIONAL PARK, TANZANIA.

JIM MOORE

*Harvard University, Department of Anthropology,
Peabody Museum, Cambridge, Mass. 02138, USA.*

INTRODUCTION

Nepotistic female hierarchies have been described for a number of monkeys, and are specially well documented in rhesus and Japanese macaques. In such a system, daughters rank just below their mother in inverse age order, younger daughter outranking older. While a positive correlation between rank and female reproductive success has been demonstrated for rhesus macaques (Drickamer, 1974), no convincing arguments have been advanced regarding the adaptive significance of strictly nepotistic ranking systems.

Recently, Blaffer Hrdy and Hrdy (1976) has reported another hierarchy system, found in langurs (*Presbytis entellus*), in which female rank is positively correlated with reproductive value such that reproductively prime females outrank both very young and old individuals. In contrast to the nepotistic system, an evolutionary 'explanation' for this is suggested by W.D. Hamilton's theory of inclusive fitness, as cited by Blaffer Hrdy and Hrdy.

In this study, female olive baboons were found to have either an intermediate or an age-graded form of hierarchy in which some females rise in rank over their mother while others remain subordinate to her (see also Angst, 1975).

METHODS

Roughly 350 hours of focal sampling were obtained on the behaviour of the adult females of two troops of *Papio anubis* at Gombe National Park, Tanzania, between December 1973 and July 1974. (Three of the 27 females - Clover in Beach Troop and Delta and Yosemite in A Troop - were nulliparous and had not yet had a full adult swelling. They were classed as adults, however, on the basis of their integration into the adult hierarchy.) Demographic data on these animals have been maintained since 1966.

Position within the dominance hierarchy was assigned on the basis of a matrix determined by the direction within dyads of both (1) displacement/avoidance interactions and (2) overt aggression. 'Displacement/avoidance' refers to one individual's movement toward another resulting in the second's withdrawal; this type of interaction was commonly associated with competition for access to food or black infants, but also occurred when a dominant animal was travelling and chanced to move toward a subordinate, and in a few instances appeared to be deliberately initiated by the dominant animal for no observable reason. A sequence of submissive gestures such as 'grin, geck, crouch-present and move away avoiding' would be counted as one instance of submission. Most, but not all, aggres-

sive behaviour prompted submission in the recipient, so HW attacking DE, who flees, appears twice in the matrix - as HW directing aggression, and DE showing submission to her. It was possible for an individual to be counted as being aggressive and submissive during one interaction if she displayed gestures characteristic of both categories, but in fact this very rarely happened.

RESULTS

A Troop (12 females)

8 of a total 590 (1.4%) submissive gestures recorded fell outside a linear hierarchy; of these, 5 involved the two nulliparous females, Delta and Yosemite.

5 of 139 (3.6%) instances of aggression ran counter to the hierarchy; 3 of these were recorded when Hawaii (age 7 years) resisted displacement by her mother, and one involved Delta and the lower-ranking mother of a black infant.

Beach Troop (15 females)

5 of 418 (1.2%) submissive gestures and 2 of 119 (1.7%) aggressive gestures were not predicted by the hierarchy; two of the submissions and one of the aggressions involved the nulliparous female Clover. Comparison with a hierarchy determined simultaneously by a different group of researchers (L. Nowell, pers. comm.) indicates a possible nonlinear relationship among females 11-14, such that 14 > (outranked) 11 > 12 > 13 > 14 (females 11 and 12 were not seen to interact with 14 by this author).

The seven mother-daughter pairs studied and their ranks are shown below. A rank of 1 corresponds to the alpha position, etc. Birth-dates are in parentheses.

A Troop	HO - 1 (post prime)	Beach Troop	AZ - 3 (post prime)
	HW - 2 (Nov. 1967)		AR - 4 (c. 1963)
	DL - 12 (old)		AZ - 3 (post prime)
	DE - 5 (Nov. 1968)		AP - 2 (c. 1967)
	YA - 11 (old)		CF - 13 (old)
	YO - 10 (Nov. 1968)		CL - 8 (June 1969)
			MR - 11 (post prime)
			MG - 12 (c. 1966)

In four of the seven mother-daughter pairs the daughter outranked her mother, while in the other three she ranked just below her. Note that of the three 'old' mothers, two (DL and CF) ranked more than 4 steps lower than their daughters, while the four 'post prime' mothers differed from their daughters by only one step. In addition, analysis of the A Troop matrix showed that significantly more aggression existed between individuals of similar than disparate rank (see Bernstein, 1971), possibly an indication of competition and potential instability of the hierarchy.

AGGRESSIVE TO/RECEIVES SUBMISSION FROM

	HO	HW	NA	ES	DE	UT	SB	LI	AM	YO	YA	DL
HO		3										
HW	9 4			1								
NA	2 3	24 4										
ES	5 3	30 10	14 4									
DE	3	22 6	18 2	16 1				3 1				
UT	3	10	5	11	13 2		1			1		
SB	2 1	2	1	3	7	10 4			1 1			
LI	2	11 3	16 2	37 4	13 2	7	7					
AM		3	2 1	11 3	8	6 4	3	4 1				
YO	2 1	6	7 1	19 8	22 3	15 9	1 1	24 3	16 5			1
YA	1	4 1	4 1	4 1	5 3	13 5	4 1	17 4	11 4	2 3		
DL	1	9 3	6 1	10 1		10 1		11 1	7 2	10 5		

A TROOP FEMALES (5/'74 - 7/'74)

Figure 1. The numeral in the upper left of each cell represents the number of times the female on the horizontal axis received submissive gestures from the one on the vertical axis; the lower right, the number of aggressive bouts directed by the individual on the horizontal axis toward the one on the vertical axis.

DISCUSSION

In addition to whatever interspecific predation they may be subject to, langurs sometimes experience a high rate of infanticide by males joining a group; This can be at least partly responsible for infant mortality rates of up to 83% over a period of several years (Blaffer Hrdy and Hrdy, 1976). This is by definition a circumstance in which troop females are alone in defending infants from a predator: the males, so important in troop defense among baboons and macaques, are here the source of danger. This pressure has apparently been great enough for kin selection to lead to concentration of reproductive effort in the prime-age females of a genealogy, with older individuals taking on the role of troop defense that has been vacated by the males.

Among olive baboons, predation/infanticide is a comparatively less serious problem for females, due to the protective role of the adult males; and the age grading of the hierarchies at this site was incomplete.

The existence of a partially age-graded hierarchy system in a species otherwise so behaviourally similar to Japanese and rhesus macaques may indicate a need for evaluation of their hierarchies both in terms of theoretical explanations for nepotism and with reference to interpopulation differences in exposure to predation, troop size, and other potential factors affecting hierarchy type.

ACKNOWLEDGEMENTS

I thank R. Wrangham, S. Blaffer Hrdy, L. Nowell, J. Goodall, J. Deag, the watu wa Gombe, and Clover, Delta, and Yosemite for their various contributions.

REFERENCES

- Angst, W. (1975). In "Primate Behavior", (L.A. Rosenblum, ed.), vol. 4, pp. 325-388, Academic Press, New York.
- Blaffer Hrdy, S. and Hrdy, D. (1976). *Science, N.Y.*, 193, 913-915.
- Bernstein, I.S. (1970). In "Primate Behavior", (L.A. Rosenblum, ed.), vol. 1, pp. 77-109, Academic Press, New York.
- Drickamer, L.C. (1974). *Folia Primatol.*, 21, 61-80.