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Agonistic Interactions of Juvenile Savanna Baboons
I. Fundamental Features

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With 3 figures

Abstract

19 juvenile members of known genealogies in two wild baboon groups were studied over a 16-month period to compare the ontogeny of agonistic experience and dominance relations for males and females. Juveniles of all age-sex classes were disproportionately likely to receive aggression from and submit to adult males per unit of time spent in proximity. This pattern intensified with increasing juvenile age. With age, juvenile females more often submitted to unrelated adult females from higher-ranking families, whereas this was not true for juvenile males. All juveniles received aggression from older group members more often during feeding than was expected by chance. High rates of agonistic interaction with unrelated adult females accounted for old juvenile females (3—5.5 years-old) interacting agonistically more frequently than male age peers and young juveniles of either sex (1—2.5 years-old). Adult females were also more aggressive toward females among young juveniles, suggesting that adult females target females among juveniles for aggression and resistance to rank reversal. Within juvenile age groups, males dominated all females and all younger males, irrespective of maternal dominance status. Dominance relations among female age-peers were generally isomorphic with relations among their mothers. No juvenile targeted any older male for rank reversal. Males targeted all older females, whereas females typically targeted only older females from families lower-ranking than their own. The strong sexual dimorphism in adult body size in baboons may explain why juvenile males' dominance relations with peers and adult females are not structured along lines of family membership as is true for the less dimorphic macaques. Acquisition of higher agonistic status probably allows juveniles of both sexes to increase their success in within-group feeding competition during late stages of juvenility, which, in turn, could affect important life-history traits such as age at menarche and adult body size.

Introduction

The agonistic interactions and dominance relations of adult cercopithecine monkeys have been primary foci of behavioral research on primates for more than twenty-five years (e. g., KAWAI 1958; DEVORE 1965; SADE 1967, 1972; HAUSFATER 1975; DE WAAL 1977, 1986; BERNSTEIN 1981; STRUM 1982; BERNSTEIN & EHARDT

1985; SAMUELS et al. 1987). In vervets *(Cercopithecus aethiops)*, macaques, and savanna baboons, males emigrate from their natal groups around puberty and appear to depend primarily on their abilities to win dyadic fights with male peers to acquire high dominance status in the groups into which they transfer (HAUSFA-TER 1975; SUGIYAMA 1976; DITTUS 1977; PACKER 1979 a, b; CHENEY 1983). In contrast, females of these species typically remain in their natal groups through-out their lives and 'inherit' dominance status adjacent to their adult female kin during prereproductive development (KAWAI 1958; KOFORD 1963; CHENEY 1977; WALTERS 1980; HORROCKS & HUNTE 1983). Dominance relations among adult males are unstable, often changing over periods of months, weeks, or even days (HAUSFATER 1975; PACKER 1979 b; TILFORD 1982). Male-male agonistic interaction is sometimes violent and occasionally results in serious wounds inflicted by canine teeth (HAUSFATER 1974; but see ROWELL 1972). In contrast, the interfamilial dominance relations of females are often stable over periods of many years and fights among free-ranging females less commonly result in wounds as serious as those that occur among males (MISSAKIAN 1972; SADE 1972; HAUSFATER et al. 1982; BRAMBLETT et al. 1982; but see SAMUELS et al. 1987).

Studies of Japanese macaques *(Macaca fuscata)* were the first to show that immature male and female macaques gradually assume dominance status adjacent to their mothers in their natal social group (KAWAI 1958; KOYAMA 1967). To assert dominance over older group members, juvenile macaques first rely on support from their mothers and other adult female kin during agonistic encounters. By puberty, they are able to dominate the adult and immature members of lower-ranking families without support from kin (see BERMAN 1980; DATTA 1983 a, b and references cited below for description of this system of rank inheritance in rhesus macaques [*M. mulatta*]). Dominance relations among same-age juveniles are transitive and isomorphic with dominance relations among their mothers. By two to three years of age, males and females become dominant to older sisters but may remain subordinate to older brothers. The serial acquisition of rank by youngest females over older sisters has been termed "youngest ascendancy" (DE WAAL 1977). Rank relations among unrelated adolescent males and between adolescent males and adult females are also determined in part by maternal dominance status (KOFORD 1963; MISSAKIAN 1972; SADE 1972; TILFORD 1982). Finally, young adult males able to maintain high status initially conferred by familial membership disperse from their natal groups later than lower-ranking peers (MISSAKIAN 1972; DRICKAMER & VESSEY 1973; MEIKLE & VESSEY 1981).

Far less information is available on the ontogeny of dominance relations in savanna baboons, and some critical data are missing. In particular, inadequate data are available to compare development in dominance relations for juvenile males and females. CHENEY (1977, 1978) reported that relative ranks among immatures of similar age *(Papio cynocephalus ursinus)* were isomorphic with those among their presumed mothers. In contrast, LEE & OLIVER (1979) found domi-nance status among juvenile males *(Papio c. cynocephalus)* to depend primarily on body size, with larger males dominating smaller males, whereas interactions between males and females seemed to be decided complexly by participants' relative body sizes, family ranks, and the support of presumed siblings. In both

studies, males and females initially assumed status among adult females adjacent to their presumed mothers, whereas LEE & OLIVER (1979) noted that young males the size of adult females could supplant most of them.

In vervets, macaques, and baboons, the aggression and agonistic support juvenile females receive from adult females reinforce the development of dominance relations along lines of familial membership (e. g., WALTERS 1980; BERMAN 1983; DATTA 1983 a; HORROCKS & HUNTE 1983; NETTO & VAN HOOFF 1986). In vervets and macaques, the same seems to be true for juvenile males. The preliminary data for baboons suggest that rank-acquisition processes for juvenile males in this species may differ. Males' relative abilities to intimidate opponents in dyadic interactions may play a considerably stronger role in determining the extent of males' rise in rank among members of their natal social groups.

The broad similarities in natural history exhibited by vervets, macaques, and baboons suggest that differing degrees of sexual dimorphism in adult body size may lead to differences in the development of agonistic relations for pre-pubertal males. In savanna baboons, adult males often weigh more than twice as much as adult females, whereas in rhesus and Japanese macaques and in vervet monkeys, males typically outweigh females by only 10 to 25 % (CLUTTON-BROCK & HARVEY 1977; COELHO 1985; ALTMANN & ALBERTS 1987). As a likely consequence, some adult females dominate some adult males in groups of macaques and vervets (KAWAMURA 1958; SADE 1967; DE WAAL & LUTTRELL 1985). Also, adult female macaques and vervets commonly collaborate to attack and even peripheralize adult male group members (KAWAMURA 1958; PACKER & PUSEY 1979; CHENEY 1983). In contrast, adult male baboons invariably dominate adult females and agonistic coalitions of females are less frequent and less effective against males (PACKER & PUSEY 1979). If adult females' reinforcement of matrilineally-ordered rank relations for juveniles functions primarily to help ensure that juveniles will maintain such relations *after* attaining puberty, female baboons could be expected to play a relatively small role in shaping the agonistic relations of immature males. Unlike females in the other species, female baboons are unlikely to be able to continue to influence the outcomes of males' agonistic interactions as the males approach adulthood (PACKER & PUSEY 1979). To determine whether the agonistic relations of immature male baboons are structured along lines of kinship, I collected data on the ontogeny of agonistic experience and schedules of rank acquisition in free-living juvenile male and female baboons.

Methods

Study Groups and Subjects

Two free-ranging groups of yellow baboons (*Papio c. cynocephalus*) were studied in Amboseli National Park, Kenya, over a period of 16 months (see PEREIRA 1988 for demographic composition of these two groups; see ALTMANN & ALTMANN 1970 and WESTERN & VAN PRAET 1973 for descriptions of the Amboseli ecosystem). During the study, Alto's Group ranged in size between 45 and 53 members, while Hook's Group ranged between 28 and 33 members. All members of each group were individually recognizable. In Alto's Group, matrilineal kin relations among all adult females and immatures were known except for possible relationships among the group's oldest females (see ALTMANN 1980). In Hook's Group, all juveniles' mothers and prepubertal siblings were known as was

Table 1: Study subjects: names, ages, group membership, mothers' ranks among adolescent and adult females, and h of sampling. Subjects' alphanumeric names identify age-sex class, group membership, and rank within age-sex class at the start of the study. There were 18 adolescent and adult females in Alto's Group (A) and 13 adolescent and adult females in Hook's Group (H)

		Name	Age at beginning of study (mos)	Age at end of study	Group	Mother's rank among females	h of focal sampling
Old							
Juv.:	Males	OMA1 (Hodi)	45	56	A	15	56.68
		OMA2 (Spike)	42	53	A	11	58.56
		OMA3 (Peanut)	42	53	A	16	55.02
		OMH1 (Nami)	34	45	H	13	49.40
	Females	OFA1 (Vixen)	40	51	A	7	54.63
		OFA2 (Oreo)	54	65	A	13	54.88
		OFH1 (Lona)	39	50	H	4	49.15
		OFH2 (Kupima)	39	50	H	6	50.42
		OFH3 (Lamu)	36	47	H	9	50.51
		OFH4 (Tatu)	60[a])	71	H	12	47.90
Young							
Juv.:	Males	YMA1 (Putz)	17	28	A	16	54.78
		YMA2 (Sluggo)	7[b])	18	A	15	28.25
		YMH1 (Rasta)	17	28	H	5?[c])	47.55
	Females	YFA1 (Siku)	16	27	A	1	54.83
		YFA2 (Pichka)	17	28	A	9	54.55
		YFA3 (Scherzo)	8[b])	19	A	11	27.52
		YFH1 (Sybil)	16	27	H	11	49.45
		YFH2 (Kanga)	18	—[b])	H	6	33.69
		YFH3 (Poco)	13	24	H	1	49.93
		YFH4 (Whiskey)	5[b])	16	H	3	16.39

[a]) Tatu's data were not analyzed for this report (see text).
[b]) Sampling on Sluggo and Scherzo began four mos after the start of the study, when they were 11 and 12 mos-old, respectively. Sampling on Whiskey began 7 mos after the start of the study, when she was 12 mos-old. All young juvenile subjects rarely or never suckled during the day. Kanga disappeared, 6 mos after the start of the study, at 24 mos of age.
[c]) Rasta's mother died before her dominance status among females could be determined precisely; however, she was known to outrank KU (mother of OFH2 and YFH2) and suspected, on the basis of few observations, to be subordinate to LI (mother of OFH1).

one adult sister for each of two juveniles. All adult males in each group had immigrated as adults, making their kin relations impossible to determine. Throughout this report, I use the term 'unrelated' to refer to group members known to be neither juveniles' mothers nor matrilineal siblings.

Table 1 describes the juveniles studied in each group. Despite aseasonal breeding (ALTMANN 1980), both groups fortuitously contained discrete cohorts of young (1—2.5 years-old) and old juveniles (3—5.5 years-old). Only one female (OFH4: Tatu) experienced menarche before the last month of the study; her data are excluded from all of the following analyses.

Sampling Methods

16-minute focal animal samples (ALTMANN 1974) were conducted on the h and the half-h from 07.00 to 17.30 h inclusive, excluding the noon h. Comparable amounts of each subject's data were gathered during each time of day and each month it was studied. To minimize the effects of observer-

presence while maintaining excellent observation conditions (see ALTMANN 1980), I tried to conduct all sampling standing 8 to 10 m from all animals.

During each focal sample, I scored every spatial displacement and overt agonistic interaction involving the subject. A displacement was scored whenever a stationary animal glanced toward an approaching animal not exhibiting any other social behavior and immediately moved away from it without exhibiting submissive behavior. When the approach of more than one animal led another animal to glance and move away, no displacement was scored. Overt agonistic interactions began whenever one animal directed aggressive and/or submissive behaviors toward another, and ended when either participant discontinued directing agonistic behaviors toward its opponent. When one animal ceased while the other continued, a second bout was scored. All interactions observed from their beginning to end outside of focal samples were recorded *ad libitum* (ALTMANN 1974).

For each encounter scored, all aggressive (A), submissive (S), and agonistically neutral behaviors (O) exhibited by each participant were noted using the behavioral definitions used previously at this site (HAUSFATER 1975; ALTMANN 1980; WALTERS 1980). Each bout was then summarized, ascribing each participant an A, an S, an AS or an O (no agonistic behavior) to denote which types of behaviors it had expressed. Bouts in which one participant emitted only aggressive behavior or no agonistic behavior while its opponent emitted only submissive behavior (A—S and S—O bouts) are referred to as *decided* agonistic interactions (HAUSFATER 1975). All other bouts (e. g., A—O, A—AS) are considered *undecided*. Only dyadic agonistic interactions are considered here; the interactions of those subjects that involved more than two participants are discussed elsewhere (PEREIRA 1984, 1986, in prep.).

Objective scores of intensity and context were recorded for every agonistic interaction scored during the last quarter of the study (1038 focal samples). Three levels of intensity are considered here. A score of 1 indicated that the aggressor threatened without making contact. A 2 denoted that contact during aggression entailed only a "hit", "push", or "grab" lasting less than 3 s. Higher intensity scores were recorded if longer "grabs", "hold downs", or "bites" occurred. The context of aggression was scored as "feeding" if one or both participants had been feeding anytime during the previous 10 s and neither had interacted with any other group member during that period. If aggression occurred while the recipient was gazing at, approaching, or interacting with a third animal that was within 3 m, the mode of interaction and the identity of the third party were recorded as the context.

Finally, beginning 1 min after the onset of each focal sample, the identities of all group members within 3 m of the focal subject were recorded at 2-min intervals. In certain situations, it was sometimes impossible to collect these point (instantaneous) samples (ALTMANN 1974) and still maintain a continuous record of behavior (e. g., during group running or foraging in a dense bush or tree). To guard against over-representation of easily-collected data (e. g., "no neighbors" and older, larger neighbors), I never collected point samples in such situations.

Tabulations and Statistical Analyses

For all tabulations concerning relative status within dyads, data on displacements were combined with data on decided agonistic interactions. For virtually all dyads, the two measures revealed the same directionality of aggression and submission, and in most cases they were both unidirectional. Rates of interaction were evaluated using only data from focal samples. Classes of juveniles were compared using a single score from each individual: number of acts divided by the appropriate total time observed (ALTMANN & ALTMANN 1977). To adjust these rates to account for the different amounts of time subjects spent in proximity to a given class of group member, each subject's score was divided by the number of members of that class that appeared in proximity per point sample.

The Mann-Whitney T test (MOSTELLER & ROURKE 1973) was used to evaluate simple age and sex differences. Stepwise multiple regressions were employed to evaluate simultaneously effects of juvenile age, sex, and the interaction of these two variables (age-sex) on rates of receiving aggression from older group members. Exploratory analyses in these instances indicated comparable variance in data from all age-sex classes. The Wilcoxon test (MOSTELLER & ROURKE 1973) or the sign test was used to evaluate paired data. All statistical tests were two-tailed with the alpha-level set at 0.05. Because information on context and intensity was recorded for only a small number of interactions, no effort was made to evaluate the statistical significance of patterns observed. For all comparisons using data from both social groups, patterns within each group were first ascertained to be the same.

Table 2: Frequencies of aggression. Median individuals' scores and range for each age-sex class

	Agonistic interactions per obs. h	% interactions that involved more than two participants	% interactions that were undecided	% interactions[a]) undecided, omitting A—O interaction
Old juv. males	1.97 [1.58—2.66]	4.0 [2.5—11.3]	14.4 [5.1—18.0]	6.2 [3.4— 9.0]
Old juv. females	2.58 [1.84—3.26]	2.5 [2.2— 3.1]	14.2 [12.4—24.5]	10.6 [0.0—11.9]
Young juv. males	1.98 [1.50—2.60]	3.8 [2.7— 7.1]	18.2 [14.7—22.3]	6.5 [4.9— 9.9]
Young juv. females	2.24 [1.16—3.36]	7.2 [0.0—12.1]	19.0 [13.4—29.5]	4.0 [0.0— 8.7]

[a]) Undecided interactions are shown with and without A—O type interactions because many A—O interactions occurred when 'aggressors' were 10 to 20 m from the animals to whom they directed threat signals; object animals often appeared unaware of these threats, and these interactions probably had less impact on developing dominance relations than any other class of interaction.

Results

Frequencies of Aggression Involving Juveniles

Juveniles engaged in one to three overt agonistic interactions per h, and old juvenile females interacted agonistically more often than did other juveniles (Table 2; stepwise regression; only variable selected, age-sex: $F = 4.63$, $r^2 = 0.21$, $p < 0.05$). Few of juveniles' agonistic encounters were undecided (median [range]: 5.4 % [0.0—11.9]), and few involved more than two participants (3.6 % [0.0—12.1 %]).

Per capita, old juveniles most often conflicted with adolescents and adults, while young juveniles most often conflicted with old juveniles. When rates of aggression were compared to time spent in proximity, however, different patterns emerged (Fig. 1). All juveniles received aggression from and directed submissive signals toward adult males more often than expected from frequencies of association. Juvenile females also submitted to unrelated adolescent males disproportionately frequently per time spent in proximity. Only old juvenile females interacted agonistically more often than expected with unrelated adult females. Finally, aggression occurred among unrelated juveniles only as or considerably less often than expected on the basis of frequencies of association. Agonistic interactions with infants were too rare to be considered.

Effects of Kinship

Every old juvenile interacted agonistically with its mother considerably less often than with unrelated adult females per capita (sign test, $N = 9$, $p < 0.005$). The same was true for all five young juveniles that never made attempts to suckle briefly during the day. Juveniles from each of the four age-sex classes interacted agonistically less often with juvenile siblings and adolescent male siblings than per capita with unrelated individuals of the same age-sex classes (sign test, $N = 5$, $p = 0.06$). Adolescent sisters were not invariably such infrequent opponents for either juvenile males or females.
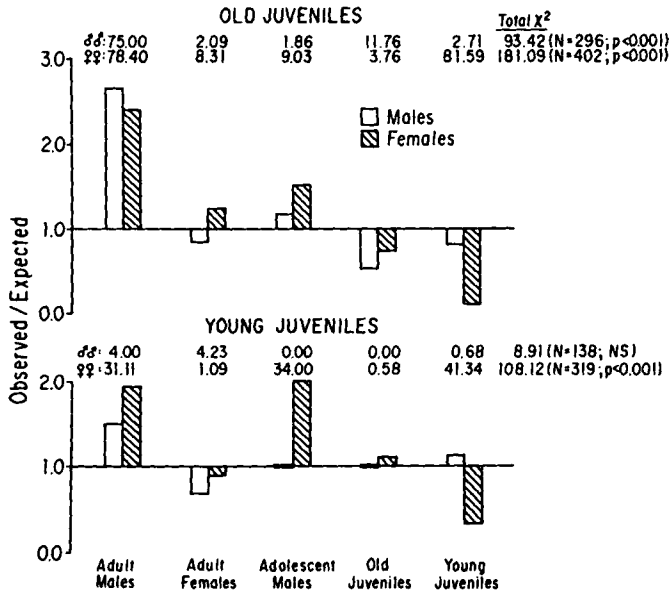
Fig. 1: Distributions of aggression between juveniles and five classes of unrelated group members relative to amounts of time spent in proximity. Bars show the proportions of expected values represented by observed values. For each subject, expected values were derived from its relative frequency of association with each neighbor class. Observed and expected values were summed within juvenile age-sex classes. Chisquare values for individual cells appear over bars

Effects of Age and Sex on Rates of Interaction with Older Group Members

With increasing age, juveniles of both sexes progressively more often submitted to adult males, despite the fact that young juveniles spent more time near adult males than did old juveniles (PEREIRA 1988) (Fig. 2). Potential effects of paternity could be evaluated only for the young juveniles of Alto's Group (see criteria used to identify "possible" and "probable" fathers in PEREIRA 1988). All five young juveniles in Alto's Group were displaced by and displayed submission toward their probable fathers less often than with any of the other five males. Also, all five submitted to their possible fathers (N = 3) less often than they did to any of the three immigrant males, despite being near their possible fathers much more often.

Adolescent males, like adult males, displaced old juveniles more often than they displaced young juveniles ($r^2 = 0.23$; p < 0.02). Again, the age difference was even stronger after accounting for frequencies of association. Unlike adult males, adolescent males did not evoke submissive behavior from old juveniles more often than from young juveniles, and they did evoke submission from old juvenile females more often than from old juvenile males (Mann-Whitney test, N, M = 4,5, T = 10, p < 0.02).

Juveniles of both sexes were displaced more often by adolescent males than by adult males per unit of time spent in proximity (Wilcoxon test, N = 19, W = 36, p < 0.02), but less frequently exhibited submission to the adolescents than to the adults (Wilcoxon test, N = 19, W_s = 43, p < 0.05). Kin relations were
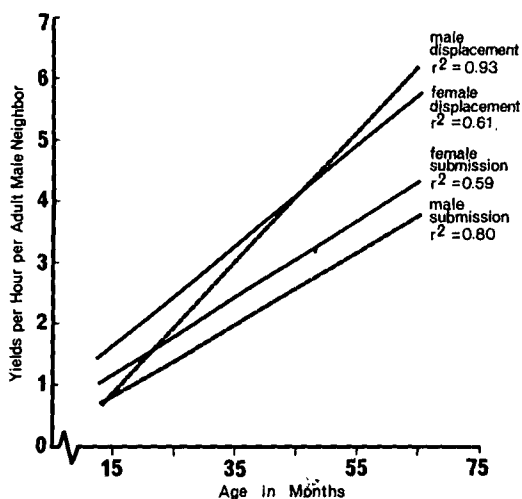
Fig. 2: Rates at which adult males displaced and evoked signals of submission from juvenile males and females per unit of time spent in proximity (within 3 m). The r^2 values show for juveniles of each sex the proportion of variance explained by juvenile age alone. Stepwise multiple regressions identified juvenile age as the only significant variable (versus Sex, Age-sex, and Group membership); displacements (both sexes combined): F = 40.27, multiple r^2 = 0.70, p < 0.00001; submission: F = 26.82, multiple r^2 = 0.61, p < 0.0001). Due to the close proximity of the four regression lines, data points are omitted to facilitate comparison of age changes in rates of displacement and submission for males and females

unlikely to have reduced rates of aggression from adolescent males. Only two of 10 subjects had a brother among the five adolescent males in Alto's Group. In Hook's Group, one of the two adolescent males was known to be unrelated to any juvenile.

Juveniles' agonistic relations with unrelated adult females differed sharply from their relations with older males (Fig. 3). Juvenile females' rates of displacement by and submission to adult females from higher-ranking matrilines increased smoothly with age, whereas this was not true for juvenile males. Also, rates of displacement were higher for females than for males in both age classes. All age and sex differences were also apparent before accounting for frequencies of association.

Although old juvenile males' rising status among adult females (see below) accounted in part for their relatively low rates of submission, juveniles' interactions with adult females from lower-ranking matrilines suggested that adult females were also generally less aggressive toward juvenile males than females (Table 3). For example, young females received aggression from females from lower-ranking families more often than did young males, although neither males nor females in this age class can effectively physically challenge or resist aggression from adult females by themselves. Young males and females spent comparable proportions of time in proximity to unrelated adult females (PEREIRA 1988), and young females were supported by their mothers during conflicts with females from lower-ranking families whereas young males were not (PEREIRA 1986, in prep.).

Contexts and Intensities of Aggression Involving Juveniles

Most of the aggression that juveniles received from adolescents and adults occurred in the context of feeding (56 %, N = 89; time spent feeding, young juveniles: 47.5 %; old juveniles: 43.9 %). Several other contexts each accounted for a small amount of aggression received (e. g., muzzle sniffing, interaction with

Fig. 3: Rates at which unrelated adult females from higher-ranking families displaced and evoked signals of submission from juvenile males and females per unit of time spent in proximity (within 3 m). The r^2 values show for juveniles of each sex the proportion of variance explained by juvenile age alone. For displacements, stepwise regression selects interaction of juvenile age and sex (Age-sex) as first variable ($F = 27.33$, $r^2 = 0.65$, $p < 0.0001$) and accepts juvenile sex to explain significant additional variance (F-to-enter Sex $= 34.47$, $p < 0.004$, F for two variable model $= 61.39$; multiple $r^2 = 0.90$, $p < 0.00001$). For submissions, stepwise regression selects only the Age-sex interaction variable ($F = 67.55$, multiple $r^2 = 0.82$, $p < 0.0001$)
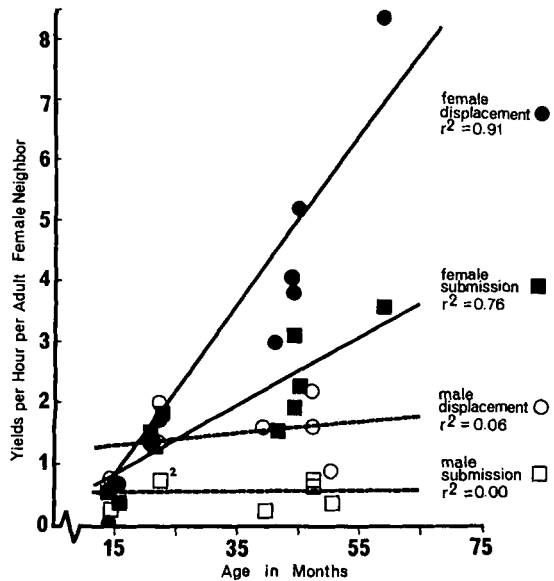
infants, redirected aggression). Adult males used the least intense forms of aggression against juveniles. Only 10 % (N = 20) of aggression from adult males included any contact (in both cases, the briefest forms of contact). In contrast, 50 % of aggression from adolescent males (N = 14) and from unrelated adult females (N = 52) entailed contact, and much of that contact exceeded the briefest forms (adolescent males: 43 %, N = 7; adult females: 35 %, N = 26).

Most aggression by juvenile males against unrelated juveniles and adult females also occurred during feeding, whereas this was not true for aggression by juvenile females (versus other juveniles, males: 73 %, N = 56; females: 32 %, N = 50; versus adult females, males: 50 %, N = 24; females: 30 %, N = 37). A related pattern concerns proportions of juvenile aggression for which context was impossible to ascribe. No context was ascribable for 27 % (N = 63) of aggression by juvenile females against old juvenile and adult females, whereas this was true for only 7 % (N = 41) of male aggression against these opponents.

Table 3: Numbers of juveniles of each age-sex class observed to submit to unrelated adult females from lower-ranking matrilines

| | Young juveniles | | Old juveniles | |
	males (N = 3)	females (N = 7)	males (N = 3)	females (N = 5)
Displaced during focal sampling	0	3	0	2
Lost decided agonistic interactions during focal sampling	1	5	0	1

Juvenile males were more likely than juvenile females to initiate contact during aggression (versus old juveniles, males: 41 %, N = 17; females: 8 %, N = 26; versus adult females, males: 46 %, N = 24; females: 27 %, N = 37). Having initiated contact-aggression against adult females, however, females were more aggressive than males (contact exceeding briefest forms, females: 60 %, N = 10; males: 27 %, N = 11).

Dominance Relations Among Juveniles

Dominance relations among the old juveniles in each social group were transitive (linear; Tables 4, 5; chance probability < 0.05; APPLEBY 1983). Ranks among old juvenile females were isomorphic with those among their mothers. In contrast, males in this age group invariably outranked all younger male peers and all female peers, irrespective of maternal ranks.

Dominance relations among the young juveniles in each social group were also transitive (chance probability < 0.02), but not as predictable as those among old juveniles. In Alto's Group, YFA3 targeted for rank reversal all females of matrilines ranking lower than her young adult sister who, three years earlier, had achieved status above adult females from two matrilines outranking her own (HAUSFATER et al. 1982; SAMUELS et al. 1987). Thus, YFA3 came to dominate YFA2 during the study (Table 4). In Hook's Group, young juvenile females ranked nearly in reverse order of maternal rank (Table 5). YFH1, daughter of the eleventh-ranking of 13 adult females, strongly dominated all three of her female peers whose mothers ranked 6, 1, and 3, respectively. Although YFH2 did not often interact agonistically with the remaining two young females, she was considered superior in rank because she dominated aggressive play in these dyads. Directionality in aggressive play was nearly a perfect predictor of agonistic dominance relations across all juvenile dyads (PEREIRA 1984).

As among old juveniles, young juvenile males outranked their female peers, irrespective of maternal rank (Tables 4, 5). One exception occurred when the young daughter of the top-ranking female in Alto's Group (YFA1) temporarily maintained an undecided relationship with YMA2 just after his weaning (see also Table 1).

Interactions between immature age classes revealed that juvenile males dominated all immatures younger than themselves, and young juvenile males acquired dominance over old juvenile females, irrespective of maternal dominance status. Data on undecided interactions (i. e., A—AS bouts) indicated that even old infant males (10—12 mos-old) occasionally begin to dominate old juvenile females (> 3.5 years-old). Young juvenile females typically reversed rank relations only with old juvenile females from lower-ranking matrilines. YFH1, however, targeted all older females except those from her group's top-ranking matriline, and ultimately acquired dominance status above two matrilines outranking her own (PEREIRA, in prep.).

Acquisition of Rank among Peers and Adults

Every old juvenile had one or more agonistic interactions with every unrelated female in its group, whereas no young juvenile did so. Every juvenile male won more agonistic interactions than he lost with every adolescent or adult

Table 4: Decided agonistic interactions among juveniles and old infants in Alto's Group. All observed overt agonistic interactions plus displacements observed during focal samples are tabulated. Juveniles are ordered so as to generate the fewest possible contradictions to linear hierarchies within age-classes. Winners of conflicts are listed to the left. Mothers' ranks among adolescent and adult females are in parentheses; for YFA3, mother's rank is followed by her unusually high-ranking adult sister's rank

	(15) OMA1	(11) OMA2	(16) OMA3	(7) OFA1	(13) OFA2	(16) YMA1	(1) YFA1	(14) YMA2	(11/6) YFA3	(9) YFA2	(15)[a] HUGOm	(10) CYMBm	(12) GRETf
OMA1 (15)	—	93	55	48	77	71	45	25	24	66	5	8	1
OMA2 (11)		—	46	29	73	87	48	18	20	48	8	6	2
OMA3 (16)			—	35	67	6	18	4	11	46	1	3	.
OFA1 (7)				—	74	.	.	4	3	27	.	.	2
OFA2 (13)		1			—	13	2	5	2	7	1	.	.
YMA1 (16)				40		—	45	50	19	52	11	9	2
YFA1 (1)				14	14		—	4	12	25	1	5	4
YMA2 (14)				3	1	1	2	—	17	16	10	5	1
YFA3 (11/6)					1				—	7	3	.	3
YFA2 (9)				3				7		—	.	.	.
HUGOm (15)											—	3	.
CYMBm (10)									1			—	1
GRETf (12)													—

Table 5: Decided agonistic interactions among juveniles and old infants in Hook's Group. See explanations of data and format in Table 4

	(13) OMH1	(4) OFH1	(6) OFH2	(9) OFH3	(5) YMH1	(11) YFH1	(6) YFH2	(1) YFH3	(3) YFH4	(4)[a] LOOPm	(6) KATHf
OMH1 (13)	—	17	15	72	68	108	59	35	30	4	1
OFH1 (4)		—	49	40	.	9	7	1	2	.	.
OFH2 (6)		1	—	65	.	14	6	4	2	1	.
OFH3 (9)			1	—	.	7	.	6	1	.	1
YMH1 (5)		18	22	29	—	67	73	55	30	3	4
YFH1 (11)		1		1	.	—	75	39	25	.	3
YFH2 (6)				7			—	.	1	.	.
YFH3 (1)								—	8	.	.
YFH4 (3)								.	—	.	2
LOOPm (4)								4	3	—	.
KATHf (6)											—

[a]) Male Loop was 3 mos older than female Kath, and 3 mos younger than YFH4.

female from lower-ranking matrilines, whereas only 3 of 12 juvenile females did so. No juvenile female ever won an agonistic encounter with an older female from a higher-ranking matriline, whereas every old juvenile male won many such encounters. Finally, no juvenile ever won a fight with any adolescent or adult male.

The progress each subject made in rank acquisition is summarized in Tables 6 and 7, using WALTERS' (1980) terminology for stages of dyadic interaction observed during rank reversal. I observed the same patterns in my old juvenile female and male subjects, and during young juveniles' attempts to achieve dominance over both older juvenile and adult females (PEREIRA 1984).

Young juveniles of both sexes made greater progress reversing dominance relations with old juvenile female targets than with adult female targets. For example, AYM1 and HYM1 reached the third transitional stage or actually reversed relations in four of their five relationships with old juvenile females, whereas they progressed this far in none of their 48 relationships with adolescent and adult females (Tables 6, 7). Younger individuals also tended to be challenged first among juvenile targets. For example, three of the four young juveniles destined to reverse relations with both OFA1 and OFA2 progressed further with OFA1, who was 14 months younger but higher-ranking than OFA2 (see Table 7 for same pattern in Hook's Group).

Juvenile males rose in rank among adult females faster than juvenile females. By the study's start, the old juvenile males had become dominant to 67, 57, and 100 percent of adult females from families lower-ranking than their own, respectively, whereas the old juvenile females had become dominant, on average, to only 11 % (range: 0—43 %; Mann-Whitney test, N, M = 3,5, T = 21, p < 0.04; Tables 6, 7). By the end, each male had become dominant to every adult female from lower-ranking families, whereas only one of the five females had accomplished this. In fact, old juvenile females achieved dominance over smaller proportions of females from lower-ranking families by the study's end than had old juvenile males by the study's start (median = 60 %). Patterns of agonistic support would be expected to have counteracted this sex difference in rate of rank acquisition: old juvenile females received considerable agonistic support during rank reversals with adult females, whereas males did not (PEREIRA 1984, 1986, in prep.).

Discussion

Differential Adult Resistance to Rank Acquisition by Males and Females

As anticipated, adult female baboons in Amboseli treated juvenile males and females differently. Adult females appeared to target females among juveniles for aggression and for resistance to rank reversal. Whereas neither young juvenile males nor females are physically capable of winning dyadic fights with adult females, primarily females in this age class received aggression from adult females from families lower-ranking than their own. Also, among old juveniles, males exhibited significantly greater rates of rank reversal with females from lower-

Table 6: Progress in rank reversals for juveniles of Alto's Group. Adult females are ordered, left age-sex classes, using relative ranks evident at the start of the study. Juveniles' interactions with their study that could be expected to be permanent; E = decided relationship evident throughout study in = initial phase of rank reversal (AS—A; see WALTERS 1980); 2 = middle phase of rank reversal rank reversal completed prior to study; 0 = insufficient interaction to determine relations.

| | Adult females | | | | | | | | | | | | | | | | | |
	SP	SA	AI	DO	ST	SU	VE	NA	PR	CE	SC	GI	FA	SL	HA	PL	EN	JA
OMA1 (15)	E	3	3	3	R	R	R	R	R	R	R	R	RR	RR	0*	RR	RR	R
OMA2 (11)	E	2	3	E	R	R	R	RR	RR	R	0*	RR	RR	R	R	R	RR	RR
OMA3 (16)	E	1	1	E	R	3	R	R	R	2	2	R	3	R	R	0*	RR	RR
OFA1 (7)	D	D	D	D	D	D	0*	RR	R	3	R	2	1	3	2	2	2	3
OFA2 (13)	D	D	D	D	D	D	D	D	D	D	D	D	D	D*	R	R	3	2	R
YMA1 (16)	E	E	E	E	E	E	0	E	0	E	E	E	0	1	E	0*	0	0
YMA2 (14)	E	E	E	E	E	E	0	E	0	0	E	E	0	E*	0	0	0	0
YFA1 (1)	D*	1	0	2	2	1	0	2	3	1	3	2	0	2	0	2	1	0
YFA2 (9)	D	D	D	D	D	D	D	0	0*	1	0	0	0	0	0	0	E	1
YFA3 (11/6)[b]	D	D	0	D	D	0*	0	0	E	0	E*	E	0	0	0	0	E	0

[a] YMA2 became dominant to YFA1 and YFA2, who were nearly 1 yr older than him (see Table 1). YFA3 became dominant to YFA2, who was 9 mos older than YFA3; YFA3's adult sister, SU, outranked YFA2's mother.

ranking families, even though the males were about the same size or smaller than their female peers and less often received agonistic support (PEREIRA 1984, 1986, in prep.).

Such differential adult female behavior toward juveniles of the two sexes is likely to be the result of characteristic sex differences in baboon life-histories (see Introduction). By preventing a female from acquiring familial dominance status, a low-ranking adult female would reduce the number of females that outrank her. A more significant consequence may be that preventing rank acquisition could cause the juvenile's entire matriline to fall in status. A recent report of long-term data from Amboseli describes several cases where a decline in rank for one adult female preceded decline in rank for other females of her family (SAMUELS et al. 1987). Decline in rank and juvenile failure to achieve rank may lead to familial loss of status through the same proximate mechanism — by changing the patterns of

to right, by decreasing dominance status. Juveniles are ordered by decreasing status within mothers with asterisks, mothers' ranks in parentheses. D = decided relationship evident throughout which older animal could be expected to be targeted by the younger one for eventual rank reversal; 1 (A—A); 3 = final phase of rank reversal (A—AS); R = rank reversal completed during study; RR = All rank reversals involved younger animals becoming dominant to older animals

Juveniles									
OMA1 (15)	OMA2 (11)	OMA3 (16)	OFA1 (7)	OFA2 (13)	YMA1 (16)	YMA2 (14)	YFA1 (1)	YFA2 (9)	YFA3 (11/6)
—	D	D	D	D	D	D	D	D	D
	—	D	D	D	D	D	D	D	D
		—	D	D	D	D	D	D	D
			—	D	R	3	3	D	2
				—	1	E	R	2	E
					—	D	D	D	D
						—	2ª)	Rª)	D
							—	D	D
								—	Rª)
									—

ª) For YFA3, both her atypically high-ranking adult sister and her mother are highlighted with an asterisk.

agonistic support that occur among families of females (see WALTERS 1980; DATTA 1983 a, b; HORROCKS & HUNTE 1983; NETTO & VAN HOOFF 1986 for discussion of hierarchy-reinforcing agonistic support among families). The new, low position of the female failing to acquire or maintain family rank could cause unrelated females to perceive her kin as occupying "incorrect" positions in the hierarchy (see also WALTERS 1980).

Because dominance relationships among adult female cercopithecine monkeys can be stable for periods exceeding a decade (SADE 1972; BRAMBLETT et al. 1982; HAUSFATER et al. 1982), behavior leading to changes in status relations among matrilines could have considerable impact on female reproductive success. Benefits such as increased access to nutritive resources, decreased age at first reproduction, and decreased interbirth intervals have been associated with high rank for female Cercopithecinae (see DRICKAMER 1974; SADE et al. 1976; CHENEY et al. 1981; WRANGHAM 1981; WHITTEN 1983; ALTMANN et al. 1988; but see GOUZOULES et al. 1982). If preventing rank acquisition by a juvenile female can precipitate a decline in rank for the juvenile's entire matriline, low-ranking adult

Table 7:   Progress in rank reversals for juveniles of Hook's Group.

		PI	WI	WN	LI	NE	KU	ET	PE	LO	MO	SI	TA	NU
							Adult females							
OMH1	(13)	E	1	2	E	E	R	0	R	R	RR	2	RR	R*
OFH1	(4)	D	D	D	1*	2	R	0	R	0	RR	1	R	2
OFH2	(6)	D	D	D	D	D	D*	R	R	RR	RR	R	RR	R
OFH3	(9)	D	D	D	D	D	D	D	R	R*	R	3	RR	R
YMH1	(5)	1	1	1	1	E	2	0	2	0	2	1	2	0
YFH1	(11)	D	D	D	D	D	1	1	1	1	0	0*	1	0
YFH2	(6)	D	D	D	D	D	0*	E	1	1	1	0	1	2
YFH3	(1)	D*	0	0	0	0	0	0	0	0	0	0	0	0
YFH4	(3)	D	D	D*	0	0	0	1	0	0	E	0	0	0

[a]) These relationships are considered to have been reversed by YFH1 because juvenile females typically dominate one another according to maternal dominance status. Both YFH3 and YFH2 died before re-reversal occurred; however, YFH4 eventually attained familial dominance status among adult females, superior to the adult rank of YFH1 (ALTMANN, SAMUELS & ALTMANN unpubl. data).
[b]) YFH4 was 8—13 mos younger than the other young juvenile females.

females could be expected to resist generally rise in rank by juvenile females. Selective aggression by adult females toward females among immatures has also been reported for macaques and vervets (e. g., DITTUS 1979; SILK et al. 1981; HORROCKS & HUNTE 1983). In contrast, adult female baboons could not influence rank relations among matrilines by resisting rise in rank immature males. Immature male baboons inevitably become dominant to all adult females (see also LEE & OLIVER 1979; JOHNSON 1984), and male baboons appear to play little or no role in the maintenance of rank relations among female kin groups (JOHNSON 1984; PEREIRA, in prep.).

Adult females are also likely to be responsible for the sex differences found in peer-peer rank relations among juvenile baboons in Amboseli which have yet to be described for other cercopithecine species. Interventions by adult females in the agonistic interactions of juvenile females reinforce rank relations that are isomorphic with relations among the juveniles' mothers (baboons: CHENEY 1977; WALTERS 1980; *Macaca mulatta*: KOFORD 1963; SADE 1967; MISSAKIAN 1972; BERMAN 1980, 1983; DATTA 1983 a; *M. fuscata*: KAWAI 1958; KOYAMA 1967; *Cercopithecus aethiops*: CHENEY 1983; HORROCKS & HUNTE 1983). Recently, this

See Table 6 for explanations of symbols and format

	OMH1 (13)	OFH1 (4)	OFH2 (6)	OFH3 (9)	Juveniles YMH1 (5)	YFH1 (11)	YFH2 (6)	YFH3 (1)	YFH4 (3)
	—	D	D	D	D	D	D	D	D
		—	D	D	3	2	D	1	0
			—	D	3	D	1	1	0
				—	R	1	3	E	0
					—	D	D	D	D
						—	RR[a])	RR[a])	E[b])
							—	0	1[b])
								—	D
									—

was found not to be true for female intervention in the conflicts of juvenile males (PEREIRA 1984, in prep.). This presumably explains why juvenile male baboons in Amboseli are free from the time of weaning to dominate all female peers and younger immatures, whereas juvenile male macaques and vervets assume ranks among immatures according to familial membership. Unfortunately, previous studies of rank acquisition in macaques and vervets have not separated data on agonistic intervention by adult females in interactions involving male versus female juveniles. Consequently, it is yet unknown whether female support for and against immature males in these species reinforces inter-familial rank relations as strictly as do adult female interventions involving immature females.

If so, the present study raises the question of why female macaques and vervets reinforce peer-peer and juvenile-adult rank relations for immature males as well as females along lines of familial membership, whereas female baboons do so for only juvenile females. Degree of sexual dimorphism in adult body size may be critical. High-ranking female macaques are able to influence patterns of group membership and dominance status for adolescent and adult males (e. g., KAWAI 1958; KAWAMURA 1958; KOFORD 1963; SADE 1965, 1967, 1972; PACKER & PUSEY 1979). For example, the sons of only high-ranking rhesus and Japanese macaque females remain in the central portions of their groups following puberty, attain high rank among adult males, and sometimes reproduce prior to emigrating (KAWAI 1958; KOFORD 1963; DRICKAMER & VESSEY 1973; MEIKLE & VESSEY 1981).

There is no known comparable effect of maternal dominance status on the rank relations of male baboons. I suggest that high-ranking female macaques and vervets maximize the effectiveness of their aggression against maturing natal males by beginning to structure aggressively the males' dominance relations before the males reach puberty. In contrast, because extreme sexual dimorphism ultimately precludes female baboons from effectively using agonistic tactics to influence the behavior of mature males, female baboons are rarely able to benefit by structuring the agonistic relations of immature males.

To test further the prediction that greater adult size dimorphism reduces the extent of adult female "socialization" of immature males, it would be valuable to have detailed information about agonistic relations between adult males and females, pre-pubertal rank acquisition, and patterns of dispersal in other cercopithecine species exhibiting pronounced sexual size dimorphism, such as bonnet macaques (*M. radiata*, adult male/female weight = 1.97) or crab-eaters (*M. fascicularis*, adult male/female weight = 1.44). Preliminary data from another substantially dimorphic macaque are intriguing: BAKER-DITTUS (1985) has reported that, unlike rhesus and Japanese monkeys, juvenile male toque macaques dominate female peers irrespective of familial rank (*M. sinica*, male/female weight = 1.6).

Sex-Specific Functionality in Baboon Rank Acquisition

The foregoing discussion does not address directly the function of rank acquisition for juvenile males and females. Immatures acquire rank among peers early in life (BERMAN 1980, 1983); however, their efforts to rise in rank among adults do not begin in earnest until late in the juvenile period. What factors influence the ontogenetic timing of rank acquisition for the two sexes? Why, for example, don't juveniles wait until they are as large as adult females before fighting to effect rank reversals with them?

Critical need for high-quality nutrition late in the juvenile period may be important. In Amboseli, feeding competition between juvenile and adult baboons appears to intensify as the juveniles age. Adults displaced and evoked submission from old juveniles more often than young juveniles per unit of time spent in proximity. As the risk of receiving aggression from adults increased, these juveniles became progressively less likely to approach high-ranking adults while the adults were feeding and less likely to feed themselves while in close proximity to the adults (PEREIRA 1988). Together, the data on juveniles' agonistic interaction and spacing relations with adults suggest that adults respond to growing feeding competition from developing juveniles by becoming progressively less tolerant of juveniles' presence during foraging. Additional support for this interpretation comes from the finding that greater than expected proportions of adult aggression toward juveniles occurred in feeding contexts.

Growing adult intolerance could reduce the quality of juveniles' diets to the extent that juveniles' chances of survival would be diminished during periods when food is scarce or dispersed widely in small, rich patches (see e. g., SUGIYAMA & OHSAWA 1982; VAN SCHAIK 1983; see also WRANGHAM 1981; CHENEY et al. 1981; see also review of relevant demographic literature in ALTMANN et al. 1985). Old

juveniles presumably reduce this risk of mortality by acquiring superior domi-
nance status over some adult females, thereby increasing their success in within-
group feeding competition (see POST et al. 1980; SILK 1986).

If ranking below all adult females results in low nutritional status for
juveniles, failure to acquire matrilineal status could also delay puberty and thus
age of first reproduction for females. Poor nutrition is known to delay puberty in
human and non-human primates (EVELETH & TANNER 1976; MORI 1979; STRUM &
WESTERN 1982; SUGIYAMA & OHSAWA 1982; see also FRISCH 1974; FRISCH &
MCARTHUR 1974; BERCOVITCH 1987 a; but see BONGAARTS 1980). ALTMANN et al.
(1988) have, in fact, shown that females of low-ranking genealogies in Alto's
Group exhibit a significant delay in age of menarche and first reproduction (see
also SUGIYAMA & OHSAWA 1982). By the end of my study, the three old juvenile
females of Hook's Group attained stable superior dominance status over greater
percentages and numbers of unrelated adult females (from lower-ranking mat-
rilines) than did either of the old juvenile females of Alto's Group. The three
Hook's Group females also attained menarche about one year earlier in life
(median age: 49 mos; median age for Alto's Group: 62.5 mos). Although
relatively slow maturation would have been observed in Alto's Group if the
dietary quality of their range was relatively poor, studies preceding and following
mine failed to reveal differential nutritional experiences for members of these two
study groups (SILK 1986; STACEY 1986).

Factors influencing access to nutritive resources during the latter stages of
juvenility, such as dominance status among adult females, could also affect
eventual mating success for males. Around puberty, male baboons experience a
radical growth spurt that eventually produces the substantial sexual dimorphism
characteristic of *Papio* species (COELHO 1985; ALTMANN & ALBERTS 1987). This
growth must be supported metabolically by ample nutrition, and limited access to
food resources could dampen the magnitude and/or shorten the duration of
growth leading to final adult body size (see KERR et al. 1975, 1982; EVELETH &
TANNER 1976; MORI 1979; JONES et al. 1985 for data on reduction of body size in
primates by poor nutrition during development). When other factors are equal
(e. g., age, length of group membership, fighting skill), dominance status among
adult male baboons is likely to be correlated with body size (see e. g., PACKER
1979 b; see also VAN NOORDWIJK & VAN SCHAIK 1985), with larger males more
often occupying relatively high positions of rank. High status appears often to be
associated with male mating success during early stages of adulthood (STRUM
1982; ALTMANN et al. 1988; see also HAUSFATER 1975; PACKER 1979 b; BERCOVITCH
1987 b). Moreover, in Amboseli, high status among adult males immediately
following immigration is associated with extended residence in a group, which, in
turn, appears to be associated with superior lifetime reproductive success (ALT-
MANN et al. 1988).

It is important to recall at this juncture that juvenile baboons rise in rank
only among female group members: neither immature males nor females ever rise
in rank among older immature or adult males. This means that there is lifelong
continuity in rank relations for females, whereas for males there is a fundamental
discontinuity. The families of females with which juvenile females fight to acquire

rank are the same ones against which they will strive to maintain rank throughout adulthood. Together attaining and maintaining matrilineal rank probably comprise a basic component of females' lifelong efforts to survive and reproduce. For males, primary competition will ultimately be with other adult males, in most cases unfamiliar males met for the first time in other (non-natal) social groups.

In contrast to females, then, the primary function of rank acquisition for males appears to change between juvenility and adulthood. The preliminary data gathered on contexts of juvenile aggression are consistent with this hypothesis. Most aggression initiated by juvenile males toward peers and adult females occurred in feeding contexts, supporting the idea that the sole function of rank acquisition for juvenile males is to increase access to quality nutrition. Lower proportions of aggression by juvenile females against peers and adult females occurred during feeding and context was impossible to ascribe for larger proportions of female-initiated aggression than of male-initiated aggression. These observations support the idea that acquisition of familial rank *per se* may be most important for juvenile females, with improved access to food as one of several beneficial consequences for successful individuals. Maintenance of familial rank may be the most important consequence of rank acquisition for female cercopithecine monkeys (WALTERS 1980; DATTA 1983 a, b; see also foregoing discussion). To evaluate these ideas further, detailed information will be needed for many cercopithecine species on the social contexts of agonistic interactions and of feeding supplantations, respectively. Such data have only begun to be collected (JOHNSON 1984; SHOPLAND 1987).

Acknowledgments

Literature Cited

ALTMANN, J., 1974: Observational study of behavior: sampling methods. Behaviour **49**, 227—264.
— —, 1980: Baboon Mothers and Infants. Harvard Univ. Press, Cambridge.
— —, & S. ALBERTS, 1987: Body mass and growth rates in a wild primate population. Oecologia **72**, 15—20.
— —, S. ALTMANN, & G. HAUSFATER, 1988: Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In: Reproductive Success. (CLUTTON-BROCK, T. H., ed.) Univ. of Chicago Press, Chicago, in press.

— —, G. HAUSFATER, & S. ALTMANN, 1985: Demography of Amboseli baboons, 1963—1983. Am. J. Primatol. **8**, 113—125.

ALTMANN, S., & J. ALTMANN, 1970: Baboon Ecology. Univ. of Chicago Press, Chicago.

— —, & — —, 1977: On the analysis of rates of behaviour. Anim. Behav. **25**, 364—372.

APPLEBY, M. C., 1983: The probability of linearity in hierarchies. Anim. Behav. **31**, 600—608.

BAKER-DITTUS, A., 1985: Infant and juvenile-directed care behaviors in adult toque macaques, *Macaca sinica*. Unpubl. Ph. D. Thesis, Univ. of Maryland, College Park.

BERCOVITCH, F. B., 1987a: Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). Am. J. Primatol. **12**, 189—195.

— —, 1987b: Male rank and reproductive activity in savanna baboons. Int. J. Primatol. **7**, 533—550.

BERMAN, C. M., 1980: Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. Int. J. Primatol. **1**, 153—170.

— —, 1983: Early differences in relationships between infants and other group members based on mother's status: their possible relationship to peer-peer rank acquisition. In: Primate Social Relationships. (HINDE, R. A., ed.) Blackwell Sci. Publ., Boston, pp. 154—159.

BERNSTEIN, I. S., 1981: Dominance: the baby and the bathwater. Behav. Brain Sci. **4**, 419—457.

— —, & C. EHARDT, 1985: Agonistic aiding: kinship, rank, age, and sex influences. Am. J. Primatol. **8**, 37—52.

BONGAARTS, J., 1980: Does malnutrition affect fecundity? A summary of evidence. Science **208**, 564—569.

BRAMBLETT, C. A., S. S. BRAMBLETT, D. A. BISHOP, & A. M. COELHO, Jr., 1982: Longitudinal stability in adult status hierarchies among vervet monkeys (*Cercopithecus aethiops*). Am. J. Primatol. **2**, 43—52.

CHENEY, D. L., 1977: The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. Behav. Ecol. Sociobiol. **2**, 303—318.

— —, 1978: Interactions of immature male and female baboons with adult females. Anim. Behav. **26**, 389—409.

— —, 1983: Extra-familial alliances among vervet monkeys. In: Primate Social Relationships. (HINDE, R. A., ed.) Blackwell Sci. Publ., Boston, pp. 278—286.

— —, P. C. LEE, & R. M. SEYFARTH, 1981: Behavioral correlates of non-random mortality among free-ranging female vervet monkeys. Behav. Ecol. Sociobiol. **9**, 153—161.

CLUTTON-BROCK, T. H., & P. H. HARVEY, 1977: Primate ecology and social organization. J. Zool., Lond. **183**, 1—39.

COELHO, A. M., Jr. 1985: Baboon dimorphism: growth in weight, length and adiposity from birth to 8 years of age. In: Nonhuman Primate Models for Human Growth and Development. (WATTS, E. S., ed.) Alan R. Liss, New York, pp. 125—159.

DATTA, S. B., 1983a: Relative power and the acquisition of rank. In: Primate Social Relationships. (HINDE, R. A., ed.) Blackwell Sci. Publ., Boston, pp. 93—102.

— —, 1983b: Relative power and the maintenance of dominance. In: Primate Social Relationships. (HINDE, R. A., ed.) Blackwell Sci. Publ., Boston, pp. 103—111.

DE VORE, I., 1965: Male dominance and mating behavior in baboons. In: Sex and Behavior. (BEACH, F. A., ed.) John Wiley and Sons, New York, pp. 266—289.

DE WAAL, F. B. M., 1977: The organization of agonistic relations within two captive groups of Java monkeys, *Macaca fascicularis*. Z. Tierpsychol. **44**, 225—282.

— —, 1986: The integration of dominance and social bonding in primates. Qu. Rev. Biol. **61**, 459—479.

— —, & L. M. LUTTRELL, 1985: The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. Am. J. Primatol. **9**, 73—85.

DITTUS, W. P. J., 1977: The social regulation of population density and age-sex distribution in the toque monkey. Behaviour **63**, 281—322.

— —, 1979: The evolution of behaviors regulating density and age-specific sex ratios in a primate population. Behaviour **69**, 265—302.

DRICKAMER, L. C., 1974: A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatol. **21**, 61—80.

— —, & S. H. VESSEY, 1973: Group changing in free-ranging male rhesus monkeys. Primates **14**, 359—368.

EVELETH, P. B., & J. M. TANNER, 1976: Worldwide Variation in Human Growth. IBP Series, Cambridge Univ. Press, London.

FRISCH, R. E., 1974: Critical weight at menarche, initiation of the adolescent growth spurt & control of menarche. In: Control of Onset of Puberty. (BRUMBACH, M. M. G. D. GROVE, & F. E. MAYER) Wiley, New York, pp. 443—457.

— —, & J. W. MCARTHUR, 1974: Menstrual cycles: fatness as a determinant of minimum weight for height necessary for their maintenance or onset. Science 185, 949—951.

GOUZOULES, H., S. GOUZOULES, & L. FEDIGAN, 1982: Behavioural dominance and reproductive success in female Japanese monkeys (Macaca fuscata). Anim. Behav. 30, 1138—1150.

HAUSFATER, G., 1974: Estrous females: their effects on the social organization of the baboon group. In: Proc. Symp. 5th Cong. Int. Primatol. Soc. (KONDO, S., M. KAWAI, A. EHONA, & S. KAWAMURA, eds.) Japan Science Press, Tokyo, pp. 117—127.

— —, 1975: Dominance and reproduction in baboons: a quantitative analysis. Contrib. Primatol. 7, 1—155.

— —, J. ALTMANN, & S. A. ALTMANN, 1982: Long-term consistency of dominance relations among female baboons (Papio cynocephalus). Science 217, 752—755.

HORROCKS, J., & W. HUNTE, 1983: Maternal rank and offspring rank in vervet monkeys: an appraisal of the mechanisms of rank acquisition. Anim. Behav. 31, 772—782.

JOHNSON, J. A., 1984: Social relationships of juvenile olive baboons. Unpubl. Ph. D. Thesis. Univ. of Edinburgh, Edinburgh.

JONES, Y. D., M. C. NESHEIM, & J.-P. HABICHT, 1985: Influences in child growth associated with poverty in the 1970's: an examination of HANES I and HANES II, cross-sectional US national surveys. Am. J. Clin. Nutr. 42, 714—724.

KAWAI, M., 1958: On the system of social ranks in a natural troop of Japanese monkeys. I. Basic rank and dependent rank. In: Japanese Monkeys: A Collection of Translations. (ALTMANN, S. A., ed.) Publ. by the editor, Chicago, pp. 66—86.

KAWAMURA, S., 1958: Matriarchal social ranks in the Minoo-B troop: a study of the rank system of Japanese monkeys. In: Japanese Monkeys: A Collection of Translations. (ALTMANN, S. A., ed.) Publ. by the editor, Chicago, pp. 105—112.

KERR, G. R., M. EL LOZY, & G. SCHEFFLER, 1975: Malnutrition studies in Macaca mulatta. IV. Energy and protein consumption during growth failure and "catchup" growth. Am. J. Clin. Nutr. 28, 1364—1376.

— —, E. S. LEE, R. J. LORIMOR, W. H. MUELLER, & M. M.-K. LAM, 1982: Height distributions of U.S. children: associations with race, poverty status and parental size. Growth 46, 135—149.

KOFORD, C. B., 1963: Ranks of mothers and sons in bands of rhesus monkeys. Science 141, 356—357.

KOYAMA, N., 1967: On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates 8, 189—216.

LEE, P. C., & J. I. OLIVER, 1979: Competition, dominance, and the acquisition of rank in juvenile yellow baboons (Papio cynocephalus). Anim. Behav. 27, 576—585.

MEIKLE, D. B., & S. H. VESSEY, 1981: Nepotism among rhesus monkey brothers. Nature 294, 160—161.

MISSAKIAN, E. A., 1972: Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys on Cayo Santiago. Primates 13, 169—180.

MORI, A., 1979: Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. Primates 20, 371—398.

MOSTELLER, F., & R. E. K. ROURKE, 1973: Sturdy Statistics. Addison-Wesley, Reading.

NETTO, W. J., & J. A. R. A. M. VAN HOOFF, 1986: Conflict interference and the development of dominance relationships in immature Macaca fascicularis. In: Primate Ontogeny, Cognition and Social Behavior. (ELSE, J. G., & P. C. LEE, eds.) Cambridge Univ. Press, New York, pp. 291—300.

PACKER, C., 1979a: Intertroop transfer and inbreeding avoidance in Papio anubis. Anim. Behav. 27, 1—36.

— —, 1979b: Male dominance and reproductive activity in Papio anubis. Anim. Behav. 27, 37—45.

— —, & A. E. PUSEY, 1979: Female aggression and male membership in troops of Japanese macaques and olive baboons. Folia Primatol. 31, 212—218.

PEREIRA, M. E., 1984: Age changes and sex differences in the social behavior of juvenile yellow baboons (Papio cynocephalus). Unpubl. Ph. D. Thesis. Univ. of Chicago, Chicago.

— —, 1986: Support during agonistic interactions given and received by free-ranging juvenile male and female baboons. Am. J. Primatol. 10, 421—422.

— —, 1988: Effects of age and sex on social association in juvenile savannah baboons (*Papio cynocephalus cynocephalus*). Anim. Behav. 36, 184—204.

POST, D. G., G. HAUSFATER, & S. McCUSKEY, 1980: Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. Folia Primatol. 34, 170—195.

ROWELL, T. E., 1972: The Social Behaviour of Monkeys. Penguin, Baltimore.

SADE, D. S., 1965: Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. Am. J. Phys. Anthropol. 23, 1—18.

— —, 1967: Determinants of dominance in a group of free-ranging rhesus monkeys. In: Social Communication Among Primates. (ALTMANN, S. A., ed.) Univ. of Chicago Press, Chicago, pp. 99—114.

— —, 1972: A longitudinal study of social behavior of rhesus monkeys. In: The Functional and Evolutionary Biology of Primates. (TUTTLE, R., ed.) Aldine-Atherton, Chicago, pp. 378—398.

— —, K. CUSHING, P. CUSHING, J. DUNAIF, A. FIGUEROA, J. KAPLAN, C. LAUER, D. RHODES, & J. SCHNEIDER, 1976: Population dynamics in relation to social structure on Cayo Santiago. Yrb. Phys. Anthropol. 20, 253—262.

SAMUELS, A., J. B. SILK, & J. ALTMANN, 1987: Continuity and change in dominance relations among female baboons. Anim. Behav. 35, 785—793.

SHOPLAND, J. M., 1987: Food quality, spatial deployment, and the intensity of feeding interference in yellow baboons (*Papio cynocephalus*). Behav. Ecol. Sociobiol. 21, 149—156.

SILK, J. B., 1986: Eating for two: behavioral and environmental correlates of gestation length among free-ranging baboons (*Papio cynocephalus*). Int. J. Primatol. 7, 583—603.

— —, A. SAMUELS, & P. RODMAN, 1981: The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). Behaviour 78, 111—137.

STACEY, P. B., 1986: Group size and foraging efficiency in yellow baboons. Behav. Ecol. Sociobiol. 18, 175—187.

STRUM, S. C., 1982: Agonistic dominance in male baboons: an alternative view. Int. J. Primatol. 3, 175—202.

— —, & D. WESTERN, 1982: Variations in fecundity with age and environment in olive baboons. Am. J. Primatol. 3, 61—76.

SUGIYAMA, Y., 1976: Life history of male Japanese macaques. Adv. Study Behav. 7, 255—284.

— —, & H. OHSAWA, 1982: Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. Folia Primatol. 39, 238—263.

TILFORD, B. L., 1982: Seasonal rank changes for adolescent and sub-adult natal males in a free-ranging group of rhesus monkeys. Int. J. Primatol. 3, 483—490.

VAN NOORDWIJK, M. A., & C. P. VAN SCHAIK, 1985: Male migration and rank acquisition in wild longtailed macaques (*Macaca fascicularis*). Anim. Behav. 33, 849—861.

VAN SCHAIK, C. P., 1983: Why are diurnal primates living in groups? Behaviour 87, 120—144.

WALTERS, J., 1980: Interventions and the development of dominance relationships in female baboons. Folia Primatol. 34, 61—89.

WESTERN, D., & VAN PRAET, 1973: Cyclical changes in the habitat and climate of an east African ecosystem. Nature, Lond. 241, 104—106.

WHITTEN, P. L., 1983: Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am. J. Primatol. 5, 139—159.

WRANGHAM, R. W., 1981: Drinking competition in vervet monkeys. Anim. Behav. 29, 904—910.

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