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Agonistic Interactions of Juvenile Savanna Baboons

II. Agonistic Support and Rank Acquisition

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With 4 figures

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Abstract

19 juvenile members of known genealogies in two wild baboon groups were studied over a 16-month period. Males and females in two age classes were compared regarding third-party aggression and support given and received during agonistic interaction. Young juvenile males and females (1—2.5 years-old) were supported predominantly by their probable fathers. The adult males supported without regard to the family ranks of juveniles and their opponents. Old juveniles (3—5.5 years-old) no longer had probable fathers in their groups and rarely or never received support from adult males. Females received considerable maternal support and, with age, most often received support from unrelated adult females. Males rarely received support from either their mothers or unrelated adult females. 100 % of adult female support for and against 11 of the 12 females reinforced existing rank relations among matriline. In contrast, only about half of adult female support of males reinforced matrilineal rank relations. Juvenile females exploited aggression among adult females during rank acquisition: they supported high-ranking adults during attacks on females they had targeted for rank reversal. In contrast, males attacked adult females in support of peers or young juveniles. Females also solicited support during fights more often than males. They most often solicited adult females, whereas males directed their rare solicitations toward other males. Despite low maternal rank, one female targeted all older females for rank reversal except the adults of her group's top-ranking family. She was the only female to receive support from adult females that contradicted existing rank relations among matriline, and the only female ultimately to achieve stable adult rank above families outranking her own. Adult female baboons appear to structure the development of rank relations for juveniles in their groups. Juvenile females are typically limited to acquisition of familial status, while males are free to achieve rank over whichever group members they can independently intimidate.

Introduction

When one animal joins an ongoing fight to help another against a third, it incurs the risks associated with fighting for the other's benefit. One risk is that fights sometimes lead to changes in participants' social status, and loss of status is often associated with loss of reproductive opportunity (e.g., LeBOEUF 1974;

CLUTTON-BROCK et al. 1979; HRDY 1981). Escalated fights entail the risk of injury that could lead directly to death (e.g., GOODALL 1986: common chimpanzees, *Pan troglodytes*) or increase vulnerability to predators or disease (pers. obs.: baboons, *Papio c. cynocephalus*; ringtailed lemurs, *Lemur catta*). What benefits accrue to supporters that may outweigh these risks? Research on patterns of agonistic support within social groups can reveal likely functions of support and, thereby, shed considerable light on the nature of a species' social organization.

Poly-dyadic (hereafter, polyadic) agonistic interactions have been studied most extensively in cercopithecine monkeys, where they appear to play an important role in the acquisition and maintenance of dominance rank (WALTERS 1980; DATTA 1983 a, b, 1988). In macaques (*Macaca* spp.) and vervets (*Cercopithecus aethiops*), immature males and females first assert dominance over older group members in conjunction with aggressive support from their mothers and other female kin. As they mature, the youngsters gradually assume status among adult females adjacent to their mothers and become capable of independently dominating members of lower-ranking families (*C. aethiops*: HORROCKS & HUNTE 1983; CHENEY 1983; *M. fuscata*: KAWAI 1958; KOYAMA 1967; WATANABE 1979; *M. mulatta*: KOFORD 1963; SADE 1967, 1972; MISSAKIAN 1972; DATTA 1983 a, 1988; *M. nemestrina*: MASSEY 1977; *M. fascicularis*: DE WAAL 1977; NETTO & VAN HOOFF 1986). A similar pattern has been documented in juvenile female savanna baboons (CHENEY 1977; WALTERS 1980). On the basis of these observations, one proposed function for agonistic support in cercopithecine societies is to help immature kin acquire familial dominance status among adults (e.g., CHENEY 1977).

Networks of social support that promote acquisition and maintenance of rank, however, extend beyond close kin. WALTERS (1980), for example, studied yellow baboons (*Papio c. cynocephalus*) of known genealogies and reported that agonistic support from unrelated adult females appeared critical to young females' acquisition of familial rank. HORROCKS & HUNTE (1983) suggested that support from unrelated adult females is also important for rank acquisition in immature vervet monkeys (*Cercopithecus aethiops*; see also CHENEY 1983). DATTA (1983 a, b) and NETTO & VAN HOOFF (1986) have reported similar patterns for macaques (*M. mulatta* and *M. fascicularis*). These results suggest that inter-familial support functions to maintain existing dominance relations among families of females in cercopithecine societies (WALTERS 1980; DATTA 1983 a, b).

The potential effects of juvenile age and gender on patterns of polyadic agonistic interaction have received little research attention. Old juveniles and adolescents have been examined repeatedly because most researchers have studied the basic rank inheritance process. The agonistic relations of weanlings and young juveniles remain to be described for most species (but see BERMAN 1980 a, b, 1983; DATTA 1983 a; HORROCKS & HUNTE 1983). Also, most studies have focussed primarily on the agonistic relations of immature females. Many authors have mentioned in passing that rank acquisition for at least some males is not as strongly influenced by factors associated with maternal rank as is rank acquisition for females (MISSAKIAN 1972; SADE 1972; CHENEY 1977; LEE & OLIVER 1979; DATTA 1983 a, 1988; NETTO & VAN HOOFF 1986; see also JOHNSON 1987). This

suggests that the mechanisms, and perhaps the functions, of rank acquisition for juveniles of the two sexes differ (PEREIRA 1988a).

For this report, the polyadic agonistic interactions of young and old juvenile baboons were contrasted to describe the ontogeny of agonistic support and to determine potential functions of support for juveniles apart from the rank-acquisition process. Young juveniles are small, weak, and inexperienced; their general vulnerability is reflected by their high rates of mortality in comparison to those of older immatures (ALTMANN 1980; ALTMANN et al. 1985). Patterns of polyadic agonistic interaction were expected to differ between young and old juveniles because the two groups face different challenges to survival and pose different challenges to adults (PEREIRA 1988a, b). For example, old juveniles, due to their greater physical capacities, were expected to provide and receive more third-party aggression than young juveniles. Demographic factors also were expected to play a role. For example, young juveniles were expected to receive considerable support from their probable fathers, whereas old juveniles, whose fathers no longer resided in their groups, were expected to receive little support from adult males.

Gender differences were expected to emerge with increasing juvenile age because the life-histories of male and female baboons differ markedly with regard to growth, dispersal, and mechanisms of status maintenance among adult peers (PEREIRA 1988a). Early data suggested that maternal status influenced the outcomes of agonistic interactions for both male and female juvenile baboons (CHENEY 1977; LEE & OLIVER 1979). Recent data, however, provided contradictory evidence. In Amboseli, Kenya, adult females targeted females among juveniles for aggression and resistance to rank reversal (PEREIRA 1988a; see also DITTUS 1979, SILK et al. 1981). Consequently, males acquired rank over low-ranking adult females at younger ages than did females. Also, males became dominant to adult females from families higher-ranking than their own, beginning well before puberty (see also JOHNSON 1987). Moreover, juvenile male baboons appear to dominate female peers invariably, irrespective of maternal ranks (JOHNSON 1987; PEREIRA 1988a).

I sought to determine whether adult baboons, through agonistic intervention, establish different schedules and limits for rank acquisition by juvenile males and females. Given that, I looked to discover whether males and females respond to this "socialization" by using different tactics in seeking, exploiting, and providing agonistic support during rank acquisition.

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 mos (see PEREIRA 1988b for demographic composition of these two groups; ALTMANN & ALTMANN 1970 and WESTERN & VAN PRAET 1973 described the Amboseli baboons and their ecosystem). Alto's Group ranged in size between 45 and 53 members during the study, 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 oldest females. In Hook's Group, all juveniles' mothers and prepubertal siblings were known, as was 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.

Table 1 describes the juveniles studied in each group. Despite aseasonal breeding (ALTMANN 1980), both groups 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 omitted.

Throughout this report, I use the term 'unrelated' to refer to group members not known to be juveniles' mothers or matrilineal siblings, except for one inferred adult sister. WI (Willy) experienced her first pregnancy during this study, occupied a dominance position (rank = 2) immediately adjacent to YFH3's mother, PI (Pindua; top-ranking), and was the most frequent grooming partner of both PI and YFH3 (other than PI; see WALTERS 1981 and PEREIRA & ALTMANN 1985 for patterns of juvenile grooming with related vs. unrelated adult females). I repeated all analyses concerned with relatedness

Table 1: Study 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 Males	OMA1 (Hodi)	45	56	A	15	56.68
	Juveniles					
	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 Males					
Juveniles						
	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).

of adult females, alternately including and excluding WI as sister to YFH3 (WALTERS 1981 and BAKER-DITTUS 1985 discuss the risks of inferring kinship from behavior among monkeys). These manipulations never changed an overall pattern of results; thus, all relevant analyses are presented with WI as the sister of YFH3.

Sampling Methods

16-min focal animal samples (ALTMANN 1974) were conducted on the h and the ½-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 overt agonistic interaction involving the subject. Agonistic interactions began whenever one animal directed aggressive and/or submissive behavior toward another, and ended when either participant discontinued directing agonistic behavior toward its opponent. When one animal ceased while the other continued, a second bout was scored. I used the same definitions of aggressive and submissive behavior used previously at this site (HAUSFATER 1975; ALTMANN 1980; WALTERS 1980). Only polyadic interactions are considered here; fundamental features of dyadic interaction in these subjects were reported previously (PEREIRA 1988a).

One conservative criterion was used to identify polyadic agonistic interactions; any baboon that directed submissive or aggressive behavior toward another baboon engaged in an ongoing agonistic interaction with a third was considered to have provided support to the third party. No assessment was made concerning which original combatant had been "winning" or "losing". The supporting individual simply had to become involved while the original interaction was still in progress. The identities and roles of each participant were recorded for all polyadic interactions observed. Only interactions observed from their beginning to end outside of focal samples were recorded on an ad libitum basis. For Alto's Group, ad libitum data were gathered by four observers during approximately 2500 h of contact with the group; only two or three observers were present during each day spent with this group. Ad libitum data from Hook's Group were gathered by only this author during about 1300 h of contact.

Analytical Approach

Because polyadic interactions were rare events, rates of support exchanged with many classes of group members could not be estimated reliably from focal samples. Therefore, I pooled data from focal samples and the ad libitum record. For each subject, the proportion of total supports given (or received) that was given to (or received from) a particular class of group member was calculated. Using the study-wide score for each subject, effects of juvenile age, sex, and the interaction between age and sex were simultaneously evaluated using two-by-two analyses of variance. All significant effects are presented. For every effect, apparent absolute rates of supports were examined to determine whether actual rates might have contradicted the result presented if more data were available. In no case did apparent rates of support contradict a result generated by an analysis of proportions.

The Mann-Whitney T test of two sample medians (MOSTELLER & ROURKE 1973) was used to evaluate separately differences between age, sex, or age-sex classes. When comparisons between small classes (e.g., young versus old juvenile males [$N, M = 3,4$]) yielded complete separation, the exact *p*-values (between 0.05 and 0.10) are given. The Wilcoxon test (MOSTELLER & ROURKE 1973) or the sign test was used to evaluate paired data. For all comparisons using data from both social groups, patterns within each group were first ascertained to be the same. All statistical tests were two-tailed (alpha-level = 0.05).

Results

Basic Patterns

In 50 h of observation, juveniles each engaged in about 100 overt agonistic interactions (mean = 93.1, SD = 22.0). Old juvenile females interacted agonistically more often than other juveniles (Table 2; see also PEREIRA 1988a). On

Table 2: Basic patterns of polyadic agonistic interaction involving juveniles

	Agon. interactions per obs. h	% interactions that were polyadic	No. of supports received per 100 agon. interactions	% polyadic interactions in which juv. were recipients of supporters' agon. behavior
Old juv. males (4)	2.0 [1.6—2.7]	4.0 [2.5—11.3]	0.9 [0.0—1.2]	37 [31—65]
Old juv. females (5)	2.6 [1.8—3.3]	2.5 [2.2—3.1]	0.9 [0.0—2.4]	19 [12—63]
Young juv. males (3)	2.0 [1.5—2.6]	3.8 [2.7—7.1]	3.6 [2.8—9.1]	33 [25—35]
Young juv. females (7)	2.2 [1.2—3.4]	7.2 [0.0—12.1]	6.1 [0.0—12.5]	5 [0—40]

Median individuals' scores and range shown for each age-sex class.

average, less than 4 % of juveniles' agonistic interactions were polyadic (no age or sex differences; median subject's score [range]: 3.6 % [0.0—12.1]; Table 2).

During polyadic interactions, juveniles gave or received support, or they received agonistic behavior from a third party. Overall, males were more likely than females to receive third-party agonistic behavior, and old juveniles were more likely than young juveniles to receive third-party agonistic behavior (ANOVA, Sex: $df = 1$; $F = 6.20$, $p < 0.03$; Age: $df = 1$; $F = 4.87$, $p < 0.05$).

Young juveniles more often received than they gave support (Wilcoxon test, $N = 8$ [2 ties], $W_s = 3$, $p < 0.05$; median scores per 50 h: supports given: 0.46; supports received: 6.60). They received significantly more support per agonistic interaction than did old juveniles (Table 2; Age: $F = 11.57$, $p < 0.005$). 8 of the 9 old juveniles gave more support than they received ($W_s = 4$, $p = 0.04$; supports given: 2.03; supports received: 0.91).

Genetic relatedness strongly influenced distribution of support. Percentages of support received from siblings exceeded mean percentages of support received from siblings' age-sex peers in nine of 10 possible comparisons (sign test, $p < 0.01$). Also, in 12 of 15 comparisons, percentages of support given to siblings exceeded mean percentages of support given to siblings' age-sex peers (sign test, $p < 0.04$). Polyadic interactions involving mothers and probable fathers are discussed below.

In summary, young juveniles engaged in polyadic agonistic interaction as often as old juveniles. During the vast majority of these interactions, the youngsters received agonistic support. Beginning at this early stage, however, males received third-party aggression during their polyadic interactions more often than females. With age, juveniles began to give more support than they received, and members of both sexes more often received third-party aggression. Siblings stood out as primary partners for the exchange of agonistic support.

Support Received

Adult Male Support

Adult males provided larger proportions of young juveniles' support than any other class of group members. In sharp contrast, adult males provided little to



Fig. 1: Percentages of support received by juveniles that came from adult males. Median individual's scores shown for each age-sex class (3 young males, 7 young females, 4 old males, 5 old females)

no support to old juveniles: 6 of the 9 old juveniles were never seen to receive support from an adult male (Fig. 1; Age: $F = 8.19$, $p < 0.02$). Juvenile spatial relations did not adequately explain this bias in male support: old juvenile males associated with adult males at rates comparable to those of young juvenile females (PEREIRA 1988b). Adult male support was not influenced by juvenile gender or matrilineal membership (Fig. 2). 68 % of male support of young juveniles ($N = 85$) was against juvenile or adolescent males, whereas these classes together comprised only 26 % (Alto's Group) and 14 % (Hook's Group) of noninfant group members.

100 % of adult male support of young juveniles came from possible fathers (males present at time of juveniles' conceptions), whereas these males constituted only 50 % and 67 % of adult males in the two study groups. In four of the five cases in which the probable father was known (Alto's Group), he was the juvenile's predominant supporter (probable father = male who consorted or copulated with juvenile's mother 5—1 days prior to detumescence of sex skin during cycle of juvenile's conception; see also HAUSFATER 1975; ALTMANN 1980; STEIN 1984). Notably, no possible father of an old juvenile still resided in Alto's Group during the study.

Maternal Support

Females received greater proportions of their support from their mothers than did males (Fig. 3 A; Sex: $F = 10.30$, $p < 0.01$). In particular, all old juvenile females received more maternal support than did any male. Juvenile spatial relations failed to explain this gender bias: young juvenile males and females associated with their mothers at comparable rates (PEREIRA 1988b). 30 % of support of daughters ($N = 30$) was against unrelated adult females (in every case, females from lower-ranking families, who represented, on average, 25 % of noninfant group members). Another 60 % was against juvenile and adolescent males. Discounting three supports against adolescent and adult males, mothers invariably assisted offspring against members of lower-ranking families (Fig. 2).

Support from Unrelated Adult Females

Old juvenile females received far more support from unrelated adult females than did male peers or young juveniles (Fig. 3 B). The age and sex effects in the

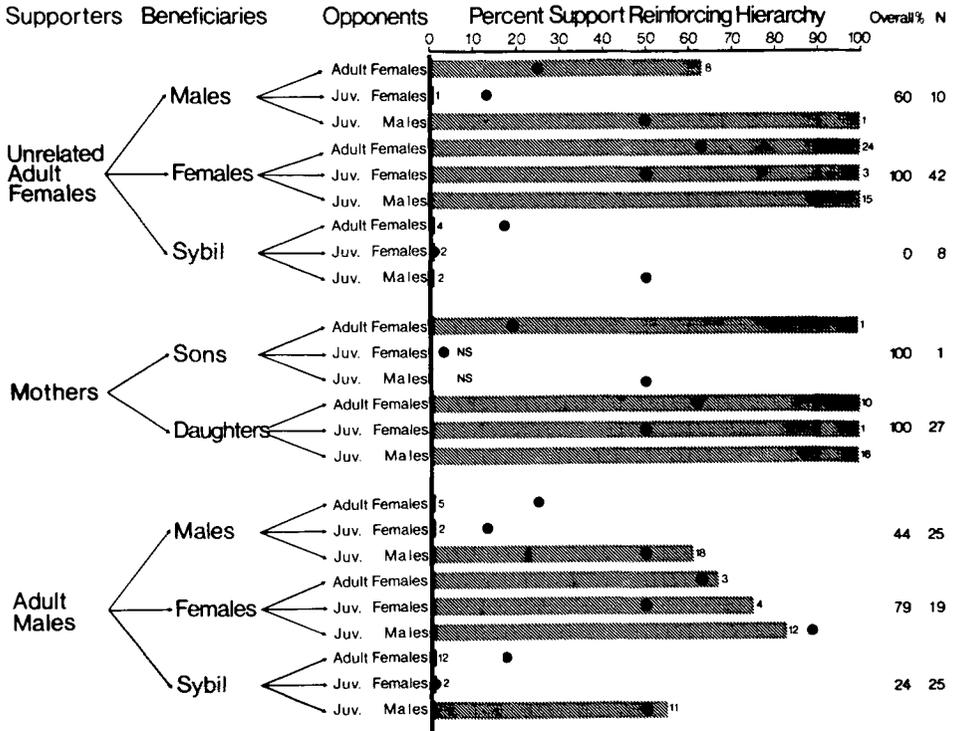


Fig. 2: Percentages of support received by juveniles that reinforced the existing hierarchy among families of females. Only interactions against unrelated group members are considered. Female beneficiaries do not include Sybil (YFH1), whose data are represented separately (see text). Dots on bars represent percentages of juvenile class-opponent class dyads in which juveniles' families outranked opponents' families. Given comparable rates of conflict with members of higher- and lower-ranking families, that percentage of support for juveniles would have reinforced the hierarchy if support had been provided without regard to fight participants' matrilineal ranks. N = number of supports

analysis of variance were due primarily to their receipt of nearly 50 % of their support from unrelated adult females (Age: $F = 6.93, p < 0.02$; Sex: $F = 4.58, p < 0.05$). 63 % of female support of old juvenile females (N = 30) was support against other adult females. In every case, the recipient of aggression was a member of a family lower-ranking than those of the juvenile and her supporter (Fig. 2). Another 30 % of female support of old juvenile females was support against juvenile males.

Only three instances of support of an old juvenile male by an unrelated adult female were observed. Each of three males was once supported against an unrelated adult female. In each case, the supporter outranked the male's opponent, but twice opponents outranked the males' mothers (see also Fig. 2).

Young juvenile males and females received comparable proportions of their support from adult females (Fig. 3 B; Mann-Whitney test, N, M = 3,7, T = 13.5, $p > 0.30$). As with old juveniles, however, adult females always supported females against members of families lower-ranking than the juveniles' (except

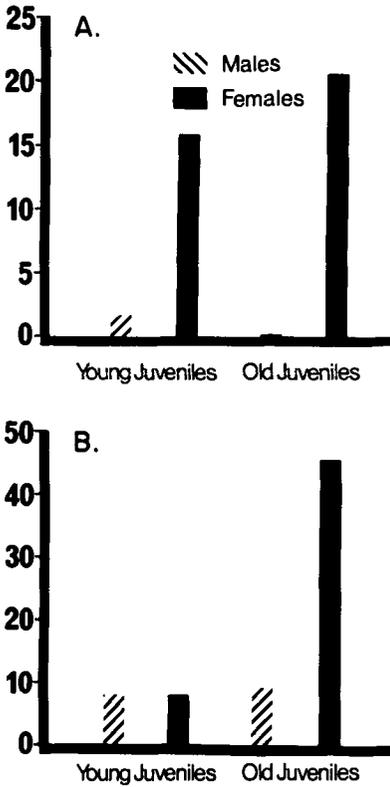


Fig. 3: A. Percentages of support that juveniles received from their mothers. Median individual's scores shown for each age-sex class (2 young males, 7 young females, 4 old males, 4 old females); B. percentages of support received that came from unrelated adult females. Median individuals' scores (N see Fig. 1)

Sybil [YFH1, see below). Again, their support of males was not restricted to this pattern (Fig. 2).

Peer Support

Finally, old juveniles received appreciable support from peers (17 % [0.0—65]), while young juveniles did not (2 % [0.0—11]). All 6 subjects that received at least 15 % of their support from peers were old juveniles (binomial test, $p < 0.04$). Females received support from both male and female peers, whereas males received peer support almost exclusively from males. Males also tended to receive more support from older immature males than did female peers. This reflects patterns of association: males spent more time near adolescent males than did females (PEREIRA 1988b).

Interactions of an Over-Achiever

Sybil's (YFH1) behavior departed dramatically from the norm. Whereas her mother had been among the lowest-ranking of Hook's Group's females throughout Sybil's life (see Table 1), Sybil clearly dominated her three female peers, whose mothers ranked 1, 3, and 6, respectively (PEREIRA 1988a). Moreover, at 18 to 24 months of age, Sybil targeted for rank reversal at least two old juvenile females (OFH1 and OFH3) and five adult females from mid- to high-ranking matriline.

Several patterns in agonistic interaction were associated with Sybil's efforts to over-achieve in dominance status. First, Sybil interacted agonistically with unrelated adult females more often and more exclusively than did any of the other nine young juveniles. Sybil also received support nearly three times as often as other young juveniles (Sybil: 53 supports received; all other young juveniles: 19 [5—34]). Only YFA1, of Alto's Group's largest and highest-ranking matriline, and the orphaned YMH1 received support at comparable rates during focal samples (per 50 h: YFA1, 7.3; YMH1, 7.4; Sybil, 6.0; median for three other young juveniles observed across entire study, 1.8).

Sybil was the only female ($N = 12$) ever to receive adult female support against females from matrilines higher-ranking than her own (Fig. 2). 7 of her 8 supports from adult females came from the three that appeared to comprise Hook's Group's top-ranking matriline. The remainder came from the adult daughter in the second-ranking matriline. Sybil also garnered an unusually large proportion of her support from her primary adult male associate (55 %; median for all young juveniles, 23 %), and an unusually large proportion of that support was against adult females (Fig. 2). Sybil had no siblings and was observed to receive no maternal support; yet, she ultimately acquired stable adult status above four females (at least two matrilines) outranking her mother (ALTMANN, ALTMANN & SAMUELS, unpubl. data).

To summarize, during the year following weaning, juveniles' most frequent supporters were their possible and probable fathers. These adult males supported males and females alike, without regard to matrilineal rank relations. Young females, but not males, also received considerable maternal support. With age, females' networks of support broadened markedly, while males' did not. 80 % of older males' support came from male peers and adolescent males. Older females received vastly increased support from unrelated adult females along with peer support and continued maternal support. Adult female support of females (except Sybil) against other females invariably reinforced existing rank relations among matrilines. In contrast, female support of males against females supported matrilineal rank relations only about half of the time. The one young female that received adult female support against females from higher-ranking families was the only female that ultimately achieved adult status above matrilines higher-ranking than her own.

Juvenile Solicitation of Support

Baboons enlist agonistic support in a variety of ways. Timely maintenance of proximity to likely supporters, greeting, grooming, and screaming all appear to increase an individual's chances of receiving support (see also GOUZOULES et al. 1984). A stereotyped behavior called "head-flagging" (HAUSFATER 1975; WALTERS 1980) is used in no other context but to solicit agonistic support from nearby group members. Whenever juveniles exhibited any of these behaviors in a way that made it obvious which group member's support was being solicited, the event and each participant's roles were recorded.

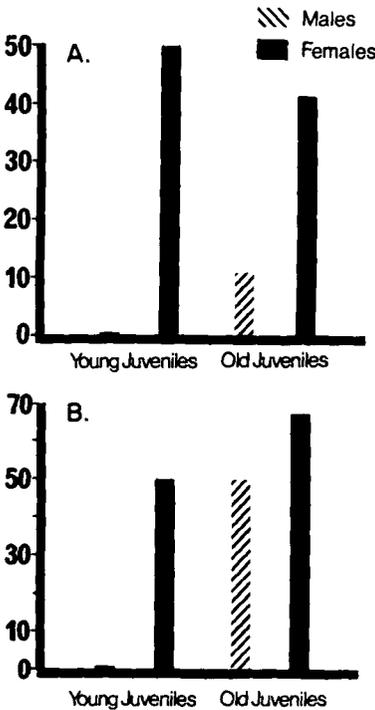


Fig. 4: A. Percentages of support given by juveniles that were support for unrelated adult females; B. that were support against unrelated adult females. Median individuals' scores (N see Fig. 1)

Both young and old juvenile females solicited support more frequently than their male peers (Sex: $F = 6.16$, $p < 0.03$; per 50 h, young males: 1 [0—2]; young females: 4 [1—13]; old males: 0 [0—1]; old females: 3 [2—4]). Also, females were more likely than males to solicit support from adult females. 61 % of females' solicitations ($N = 51$) were directed toward adult females, whereas only one male solicitation of female support was seen. The other eight male solicitations observed were directed toward adolescent or adult males.

Support Given

Juvenile females supported unrelated adult females more often than they supported any other class of group member (75 %, $N = 20$). Moreover, females both supported and supported against unrelated adult females significantly more than did their male peers (Fig. 4A: support for adult females, Sex: $F = 15.40$, $p < 0.002$; B: support against adult females, Sex: $F = 8.72$, $p < 0.02$), although every old juvenile male was engaged in rank reversal with a greater number of adult females than was any juvenile female (PEREIRA 1988a). 85 % of female support of adult females ($N = 20$) comprised support against other adult or old juvenile females, whereas this was true for only 33 % of male support of adult females ($N = 9$). Conversely, 63 % of female support against adult females ($N = 32$) was support of other adult or old juvenile females, whereas this was true for only 16 % of male support against adult females ($N = 37$). Most support by old juvenile males against adult females went to male peers and young juveniles of either sex.

Every time females joined a fight between unrelated adult females, they supported in a manner that reinforced the existing hierarchy among matriline (N = 15). In contrast, only one of males' three interventions in fights between adult females reinforced existing matrilineal rank relations.

All juveniles provided little support to their mothers. Four of the 8 old juveniles with mothers in their groups each supported them once or twice (3 males; 1 female). None of the other 13 juveniles with mother present was ever seen supporting her. Notably, the two supports OMH1 provided his mother comprised aggression toward adult females from higher-ranking matriline.

Support for Adult Females against Juveniles

Females received virtually all observed support for adolescents and adults against juveniles. 83 % of support for adult females (N = 29) was against unrelated old juveniles. Support against males (N = 14) was provided primarily by adult males (50 %) and high-ranking adult females (29 %). In each case, females were supported who outranked the mothers of their male opponents. However, females outranked males' mothers in over 95 % of conflicts between adult females and juvenile males.

Comparable amounts of support against old juvenile females were provided by old juveniles, adolescents, and adults of both sexes. All female support against juvenile females (N = 5) reinforced existing rank relations among matriline. 6 of the 7 male supports against females contradicted existing rank relations among matriline (two each by old juvenile, adolescent, and adult males). Adult females outranked the mothers of their female opponents in 65 % of observed conflicts between these two classes.

Discussion

Adult Males Promote Survival of Probable Offspring

Adult male baboons in Amboseli play a primary role in support of young juveniles. Each young juvenile in this study associated frequently with one to three particular long-term resident males in its group (PEREIRA 1988b). These males actively protected their juvenile associates from social harassment. Any of them might have been the juveniles' fathers, because they were group members when the juveniles were conceived. In four of the five cases with more data on probabilities of paternity, juveniles' most protective male associates were "probable" fathers (see ALTMANN 1980; STEIN 1984). Adult males in Alto's Group never supported old juveniles, and none was present when the old juveniles were conceived. In Hook's Group, only one male provided old juveniles appreciable support (Harvey), and he was the only male in this group known to have been present when they were conceived.

These data suggest that adult male tolerance and agonistic support of young juveniles function as paternal behavior. A competing hypothesis is that such altruism promotes the development of affiliative relations between the males and the immatures' mothers which, in turn, enhance the males' chances of mating

with those females (see e.g., SMUTS 1983, 1985). WALTERS (subm. ms.) has reported data that support the paternal investment hypothesis but not this alternate hypothesis. WALTERS compared old juveniles' relationships with (a) "godfathers" (often probable fathers; ALTMANN 1980), (b) possible fathers, and (c) impossible fathers. The godfather of four females was the only adult male that maintained strong affiliative relations with them, including grooming, agonistic support, and withholding of aggression. Moreover, males that developed affiliative relations with the juveniles' mothers only after the juveniles' conceptions did not maintain special relationships with the juveniles.

Adult male support of young juveniles was not biased on the basis of either juvenile gender or matrilineal status vis-a-vis opponents. Thus, male support does not promote juvenile rank inheritance in baboon society. High-ranking male toque macaques (*Macaca sinica*) have also been found to support young juvenile males and females equally frequently and without regard to matrilineal status (BAKER-DITTUS 1985). Interestingly, these adult males favored males among juveniles for low-cost affiliative behavior, such as approaches, hugs, and brief carries (BAKER-DITTUS 1985); this bias did not exist in the behavior of adult male Amboseli baboons (PEREIRA 1984). Whereas agonistic support of young juveniles by adult males probably functions to promote offspring survival in several cercopithecine species (also *M. fuscata*: WATANABE 1979; *M. fascicularis*: VAN NOORDWIJK pers. comm.), the significance of other affiliative behavior needs to be examined separately.

Constraints on Maternal Support

In contrast to probable fathers, mothers did exhibit a gender bias in supporting juvenile offspring: daughters received support, whereas sons did not. This result highlights important proximate factors constraining patterns of support in a baboon group. One is familial status. Due to their low rank (see Table 1), the mothers of the young males in my sample were less able to support their offspring than were the mothers of young females. Because female baboons almost never join fights against higher-ranking females (WALTERS 1980), the young males' mothers were less likely than the females' mothers to be "eligible" to intervene in support of their offspring (see also DATTA 1983 a, b; HORROCKS & HUNTE 1983; NETTO & VAN HOOFF 1986). Maternal rank may often play a sex-differentiating role for juveniles in Amboseli because low-ranking females produce more sons than daughters, while high-ranking females most often have daughters (ALTMANN et al. 1988).

Another proximate factor is the intensity of aggression received, i.e., the relative need for support. Previous analyses, for example, indicated that adult females were most aggressive toward females among juveniles. Also, low-ranking females more strongly resisted rank reversal with juvenile females than with juvenile males (PEREIRA 1988a; see also DITTUS 1979; SILK et al. 1981). Thus, support was probably needed in fewer of males' than of females' interactions with unrelated adult females. Young males also rarely needed maternal support against peers because most were female. From weaning, every male dominated all close

female peers, irrespective of matrilineal status (PEREIRA 1988a; see also JOHNSON 1987). Although young females received some maternal support against male peers (from lower-ranking families), the males received some support against the females from unrelated adult females. In contrast, juvenile females never received adult female support against females of higher-ranking matrilines (except Sybil, discussed below). Notably, YMA2's mother outranked YMA1's, but she never supported her son against his dominant male peer.

Adult Female Determination of Juvenile Rank

Following weaning, males and females experienced different "rules" governing their dyadic and polyadic agonistic interactions (see also PEREIRA 1988a). These rules, enforced by adult females, comprise social mechanisms that force females into dominance relations based on matrilineal membership (see also CHAPAIS 1988), and leave males unconstrained to assume ranks based primarily on their relative abilities to intimidate their opponents. Why would female baboons establish different rules for rank acquisition for juvenile males and females? The likely answer lies with the different life-histories of males and females.

Female baboons live out their entire lives amidst a stable set of female peers. The stability of dominance relations among matrilines depends on reciprocal supportive relations within families and hierarchy-reinforcing patterns of support among families (CHENEY 1977; WALTERS 1980; DATTA 1983a, b). Adult females probably abbreviate the period of rank instability between juvenile and adult females by supporting the juveniles frequently against adults from lower-ranking families and by supporting adults whose families outrank the juveniles'. By abbreviating the period of rank indeterminacy, adult females reduce the probability of over-achievement in juvenile rank acquisition. Over-achievement by a juvenile female might often lead to an eventual rise in rank for her entire matriline (see below). By supporting daughters against lower-ranking adult females, mothers help to consolidate their matriline within the adult female hierarchy and thereby reduce the chance of a decline in familial status (PEREIRA 1988a).

Adult female baboons cannot benefit in these ways by structuring the rank relations of immature males according to matrilineal membership. Maturing males inevitably become dominant to all adult females, typically emigrate, and appear to play no role in the maintenance of rank relations among female kin groups (WALTERS 1980; JOHNSON 1984; PEREIRA 1988a). Elsewhere, I have discussed possible reasons why adult female macaques and vervets (*Cercopithecus aethiops*) do benefit by structuring the rank relations of immature males as well as females according to matrilineal membership, despite exhibiting life histories broadly similar to those of savanna baboons (PEREIRA 1988a, in prep.).

The case history of Sybil (YFH1) is the first detailed account of a naturally-occurring breakdown in the system constraining cercopithecine females to inheritance of familial status. Frequent and diverse support contradicting matrilineal rank relations ultimately allowed Sybil to achieve stable adult status above at least two matrilines outranking her own (SAMUELS pers. comm.; 1986 status summary, J. ALTMANN, S. ALTMANN, & A. SAMUELS unpubl. data; N.B. — the long-term records show that Sybil's mother has likely never held higher rank than during

my study; thus Sybil was not targeting adult females formerly lower-ranking than her mother [see WALTERS 1980; but see JOHNSON 1987]). Most important, Sybil was the only juvenile female ever supported by adult females against females from families higher-ranking than her own.

Sybil's atypical targeting of high-ranking females for rank reversal, and receipt of support against them, comprise one way in which cercopithecine females can exceed expected limitations in life-long social status. Sybil enhanced the effectiveness of her network of support using affiliative behavior. Intense and complex polyadic interactions often ensued after Sybil initiated or escalated aggression with mid-ranking females and then used proximity, grooming, and overt solicitation to elicit support from her group's top-ranking females and her male associates. During the two years following my study, Sybil's tactics presumably became even more effective as she began to influence physically as well as socially the outcomes of such melees.

Despite her success, Sybil's behavior entailed tremendous risk — risk that presumably contributes to the rarity of observed efforts by cercopithecine juvenile females to over-achieve in rank acquisition. Several times, Sybil limped severely following fights with the much stronger, older females. I once returned to study Hook's Group and found Sybil limping with one eye bruised and swollen shut; this condition persisted for about two weeks. Her frequency of fighting with mid-ranking females during my previous period with Hook's Group suggested that these injuries resulted from such fights. Also, no other young juvenile ever received comparable injuries during my study. Impaired vision and locomotion seriously compromise a young juvenile's chances for survival in Amboseli (see ALTMANN 1980; PEREIRA 1988b).

The young female Scherzo (YFA3) and her adult sister Summer (SU) in Alto's Group have recently demonstrated, however, that over-achievement in rank acquisition may have far-reaching consequences. Years after Summer attained status above two matriline (four females) outranking her mother (HAUSFATER et al. 1982), her sister, Scherzo (this study), targeted for rank reversal all females lower-ranking than Summer (PEREIRA 1988a) and received adult female support against those females. Social dynamics initiated by Scherzo's targeting of females ranking between her mother and high-ranking sister may have promoted the additional rise in rank of her mother and oldest sister (see SC and SC-d1 in SAMUELS et al. 1987). Over the five-year period following Summer's initial over-achievement, her entire matriline rose from the bottom half to the top half of the hierarchy in a moderately large baboon group (50—60 members; SAMUELS et al. 1987).

Rank relations among matriline in Alto's Group should become extremely stable because the rank positions of females within kin groups have been consolidated (SAMUELS et al. 1987; see SADE 1972; BRAMBLETT et al. 1982; HAUSFATER et al. 1982 regarding stability of cercopithecine dominance hierarchies). In ten years, a female baboon in Amboseli can carry up to six pregnancies to term, and two or three of those infants are likely to survive to sexual maturity (ALTMANN et al. 1985, 1988). For a high-ranking female, two of these offspring are likely to be female (ALTMANN 1980; ALTMANN et al. 1985, 1988), and these

daughters "inherit" whatever benefits are conferred by high status regarding survivability and fecundity (DRICKAMER 1974; SADE et al. 1976; CHENEY et al. 1981; WRANGHAM 1981; WHITTEN 1983). In Amboseli, this includes at least earlier age at first reproduction (ALTMANN et al. 1988), a life-history trait with potentially large impact on lifetime reproductive success (COLE 1954).

Gender Differences in Response to the Challenge of Rank Acquisition

While patterns of adult female aggression and support set the stage for gender differences in rank acquisition, juvenile males and females also responded in different ways to the challenge of rank reversal with adult females. Females exploited adult females' proclivities to support them against members of lower-ranking families by resting near and grooming high-ranking females during periods of frequent or imminent fighting (PEREIRA 1984, 1988b). Also, females but not males, exploited opportunities to dominate adult females made available by aggression among adult females. They more frequently supported adult females than did males, and, in doing so, they joined fights in which targeted adults were already being intimidated. In contrast, males most often attacked adult females while the females were winning fights against juveniles.

Females also commonly solicited agonistic support, whereas males rarely did so. Perhaps males rarely solicited support because most group members previously failed to respond. Another possibility, however, is that males ultimately benefit by *not* receiving support. Skills in dyadic fighting appear largely to determine dominance status among young adult male baboons (HAUSFATER 1975; PACKER 1979). Juvenile males can create a diverse and challenging experience during rank acquisition by striving to reverse rank relations with all adult females without support. Such an experience would presumably contribute most strongly to their acquisition of fighting skills and, thereby, to their chances for relatively high reproductive success during young adulthood (STRUM 1982; BERCOVITCH 1986; ALTMANN et al. 1988).

The support males occasionally sought and received came from other males. Agonistic cooperation among immature males might provide valuable experience in coordinating attacks to repel or even defeat formidable opponents. Old male baboons form coalitions against younger males that enable them to protect themselves better and, sometimes, to defeat their opponents (PACKER 1977; STRUM 1982; SMUTS 1985; NOE 1986). Male-male cooperation prior to emigration may also initiate reciprocally supportive relationships that become important early during adulthood. Familiar males sometimes migrate together or reunite after migration (PUSEY & PACKER 1987). Early cooperative relations could facilitate agonistic coalition, expedite assimilation into new groups, and promote acquisition of relatively high status (see, e.g., MEIKLE & VESSEY 1981; TILFORD 1982).

Opportunity versus Enterprise in Cercopithecine Rank Acquisition

The importance of opportunity for cercopithecine monkeys in acquiring dominance status is becoming clear. DATTA (1983a, b) suggested that infant rhesus macaques receive aggression and support that reinforce existing rank

relations among matriline before the immatures exhibit initiative in rank acquisition (see also HORROCKS & HUNTE 1983). During my study, juvenile males rose faster and farther than females in dominance status among adult females because adult females yielded relatively readily to their efforts to rise in rank (PEREIRA 1988a). Indeed, I observed many adult females begin submitting to two year-old males, long before the males could possibly have presented any physical threat. Support received from powerful allies undoubtedly created the opportunity Sybil had for over-achievement in rank acquisition. If the high-ranking females had responded "normally" to her (by adding "punishment", rather than contributing support), she most likely would have desisted in her efforts or died due to them.

I believe, however, that Sybil's over-achievement first required enterprise. Due to the timing of this study, it is unknown when adult females began supporting her against females outranking her mother. But, Sybil dominated peers from her group's first- and third-ranking families when she was weaned (YFH3 and YFH2, PEREIRA 1988a), despite never receiving female support against them. I suggest that Sybil's persistent enterprise, unusual both in its early onset and in her targeting of older members of higher-ranking families, changed normal patterns of support, leading top-ranking females to begin supporting her against the females of mid-ranking families.

The nascent agonistic relations of weanling and young juvenile monkeys merit considerable attention in future research. Fuller appreciation of the interplay between individual enterprise and opportunities provided by the social environment will be essential to understand deeply the range of developmental and evolutionary factors involved in acquisition and maintenance of dominance status in cercopithecine societies.

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