

Which Adult Male Savanna Baboons Form Coalitions?

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*We investigated the mechanism of alliance formation among adult male savanna baboons by comparing the characteristics of males that formed coalitions frequently with males that never or seldom took part in coalitions. We observed three groups: two of *Papio cynocephalus cynocephalus* in Amboseli National Park, Kenya, and one of *P. c. anubis* in the vicinity of Gilgil, Kenya. We considered four hypotheses: (1) Males must be familiar with each other, (2) males must have an affiliative bond, (3) males must have more than average experience, and (4) the combined fighting ability of the coalition partners relative to the fighting ability of their opponent determines the likelihood that a coalition is formed. We conclude that relative fighting ability forms the key factor in coalition formation. High-ranking males do not form coalitions often, since they hardly need them. Low-ranking males rarely form coalitions, since they cannot form effective coalitions among themselves. Affinity ("friendship") may play a role as an additional factor. The relation of coalition formation with age and period of residence, which was found in several studies, can be explained largely by the correlation between these parameters and fighting ability.*

KEY WORDS: baboon; *Papio*; coalition; alliance; cooperation.

INTRODUCTION

While some adult male savanna baboons frequently form coalitions, others hardly ever do. We ask: what determines whether males form coalitions? Are males with certain individual attributes, like old age or low

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fighting ability, more likely to form coalitions than others? Or is a certain quality of their relationship, like familiarity, a prerequisite of coalition formation?

We (Noë and Sluiter, 1990) have shown that middle- and low-ranking males can improve their mating success considerably by forming coalitions. High-ranking males usually gained access to estrous females on their own; for them coalitions would imply an unnecessary obligation to share. Assuming that the lower his rank, the more a male would need coalitions, one would expect a simple, linear relationship between rank and frequency of coalitions formed. Contrary to this expectation, however, we found lower frequencies for low-ranking males than for middle-ranking males. Accordingly, it is possible that low-ranking males form few coalitions not because alliances would not be advantageous, but because they are not able to do so. We tried to find the reason for this inability, since we presupposed this to be the key to understanding the process of coalition formation. We analyzed data on coalition formation gathered in two medium-size groups of yellow baboons (*Papio c. cynocephalus*) and one large group of anubis baboons (*P. c. anubis*). In contrast to our earlier paper (Noë and Sluiter, 1990) we included all coalitions, instead of only those formed in the context of sexual competition.

Factors that Influence the Ability to Form Coalitions

In several studies on coalition formation in adult male baboons (Noë, 1992), they were formed most frequently by males that were past their prime, of middle or lower rank, and resident in their group over a relatively long period. This leads to the conjecture that two attributes of males — *age* and *rank* — and two attributes of male–male relationships — *familiarity* and *affinity* — could play an important role. We formulated four hypotheses, each based on one of these parameters.

The Experience Hypothesis

Baboon males that form coalitions are older males according to the majority of studies (Noë, 1992), implying that males need experience to form coalitions. This could in principle be general experience — *the age hypothesis* — as suggested by Smuts (1985, 1987), or specific experience in forming coalitions. In any case the prediction would be that the frequency of coalition formation would increase with age.

The Familiarity Hypothesis

In several studies (Noë, 1992), coalitions were frequently formed by males that had been in a group together for a long time. This suggests that knowing each other well is a *sine qua non* of coalition formation (Collins, 1981; Smuts, 1985; Noë, 1986). In its basic form, the familiarity hypothesis can be formulated as follows: Any two males that are members of the same group for a minimal period of time are able to form coalitions. The familiarity hypothesis is falsified if newcomers are found to be regularly involved in coalitions.

The Friendship Hypothesis

Smuts (1985) suggested that alliances are formed by males that have affiliative relationships, i.e., males with a relationship characterized by higher than average frequencies of behaviors that imply tolerance and attachment, like close proximity, low aggression, tolerance at food resources, etc. Males with affiliative relationships are likely to form a subset of the males that have a relatively long period of shared residence in the same group.

The Fighting-Ability Hypothesis

Bercovitch (1988) and Noë and Sluiter (1990) concluded that the combined fighting ability of a coalition, relative to the fighting ability of the target of the coalition, determines a coalition's success and thus the likelihood that it will be formed. Assortative pair formation can be expected if both partners seek the best possible partner, bringing partners of comparable strength together. Accordingly, we predicted that lower- rather than higher-ranking males are involved in coalition formation and that coalition partners are relatively close in rank.

Interdependency Among Age, Rank, and Period of Residence

Age, fighting ability, and period of residence are the crucial parameters in the four hypotheses. In several studies on adult male baboons, these parameters were strongly correlated (Noë, 1992). Fighting ability shows a bell-shaped relationship with age (Packer, 1979; Rasmussen, 1980; Ransom, 1981; Manzollilo, 1982; Smuts, 1985). The majority of the males leave their natal group as young adults (Altmann *et al.*, 1988) around the time they

attain their maximal fighting ability. Such a male is likely to gain a high rank in his new group (Collins, 1981; Noë, 1989; Hamilton and Bulger, 1990; this study), after which he will gradually drop in rank as he ages and new males arrive. Thus lower-ranking males tend to be older than higher-ranking ones and tend to know each other longer.

Unfortunately, we lacked sufficient information on some crucial parameters, and had to use other parameters as substitutes: period of residence for age and dominance rank for fighting ability. The parameters are valid substitutes, if they show a strong correlation with the relevant parameters. It seems reasonable to assume that dominance rank is an appropriate substitute for fighting ability in rank tests, because in such tests the magnitude of the "gap" between two males of adjacent rank is ignored. The period of residence is a good estimator for age, if males migrate only once in their life. Most groups will contain a few males that migrated more than once, which should be taken into account when the results are evaluated.

METHODS

Study Sites, Groups, and Observation Periods

We studied two groups of yellow baboons (*P. c. cynocephalus*) concurrently, usually on alternating days, in Amboseli National Park, Kenya, from December 1981 till December 1982. Alto's group (ALTO) had been under study from 1971; Hook's group (HOOK), at intervals since 1976 and on a regular basis since 1980 (Hausfater, 1975; Altmann, 1980; Altmann *et al.*, 1985). Groups sizes and compositions are in Table I. We collected data on the Eburru Cliffs group (EC) of olive baboons (*P. c. anubis*) at a site near Gilgil, Kenya, from November 1983 till November 1984. EC had been under regular observation since 1978 (Smuts, 1985; Noë, 1989). We were forced to interrupt our observations in February/March 1984. During the interruption, 11 members of the group were killed by a farm manager. The data we used in our general analyses stem from the period after March 25, with additional information from the period before the interruption.

Differences Between Sites and Consequences for the Use of Data

Amboseli is a national park with a population of baboons stabilized at a low level after a long decline (Altmann *et al.*, 1985). Gilgil is an agricultural area in which the baboon population expanded rapidly after additional water was brought in by European settlers. Some natural predators

Table I. Size and Composition of Study Groups^a

Group	Total group size	Mature immigrant males	Mature natal males	Mature females	Sex ratio mature males/females
HOOK	33-41	6-7	0	14-16	0.38-0.47
ALTO	50-55	6-8	0-1	18-19	0.33-0.47
Eburru Cliffs	95-114	5-8	7-9	34-40	0.35-0.44

^a Minimum and maximum numbers during the study.

— leopard, python, birds of prey — occurred in unknown densities, but other species had disappeared (notably lion and spotted hyena) or migrated infrequently through the area (wild dog). Natural predation on baboons was partly replaced by hunting by farmers and their dogs. Compared to natural predation, this type of hunting is biased toward the adult and subadult males. Adult males make the largest targets and are also the most notorious crop raiders. This difference between sites did not lead to an obvious difference in the adult sex ratio (Table I), but it could have affected the age composition of the adult male subgroup.

We used data gathered in Amboseli (ALTO and HOOK) as the principal data set for hypothesis testing. We used the observations of EC as a source of complementary data: We checked whether the findings for ALTO and HOOK are at least not contradicted by the EC data. This decision is based on the following considerations: (1) The Amboseli site is a more natural habitat and the groups suffered less from human interference, (2) In reaction to the severe drought during our study in Gilgil in 1984, EC deviated considerably from their normal pattern of foraging (B. Smuts, personal communication), and the conditions for observation were not as good as during our Amboseli study. Consequently, the amount of data per male is much higher for ALTO and HOOK than for EC. (3) The frequent changes in membership and the frequent splitting into subgroups of EC made many corrections for absence necessary. (4) The group sizes and visibility in Amboseli are such that for conspicuous events — sexual consortships, polyadic conflicts, and conflicts with vocalizations — the ad libitum observations were virtually focal group samples. This can not be assumed for the data on EC.

It should not be concluded that we consider Amboseli to be a 'typical' baboon habitat and the Gilgil site as not representative. First, savanna baboons are adapted to a wide variety of habitats. Second, nature reserves like Amboseli National Park tend to be founded in areas of marginal or no importance to human agriculture, which could well be marginal for baboons as well.

Males Included and Individual Codes

We included in the analysis all males that were 6 years old at the start of the study [classified as subadults according to Altmann *et al.* (1981)]. Most males show a period of rapid growth around this age, after which they are strong enough to provide a significant contribution to a coalition against an adult male. Concurrently, young males may go through a series of dominance reversals with adult males, resulting in a rapid rise in rank (Noë, 1992). We did not use data on three EC males that were present during <200 hr of observation (E9, E16, and E17) in the analyses.

We list the subjects in Table II, with dates of births and death/emigration and time elapsed since immigration. The Roman numeral in each male's code gives an indication of the male's rank.

Observational Methods and Analysis

Sampling Methods

All three groups were well habituated and could be followed on foot. We gathered data via ad libitum sampling and focal-animal sampling (Altmann, 1974). During the 20-min focal samples, we took proximity samples at 2-min intervals. During these samples, we scored all individuals ≤ 2 m from the focal male. In the Amboseli study, we also noted all males ≤ 5 m from the focal animal 2 min before sampling started. Total observation times and numbers of focal samples are in Table II.

We supplemented the data on the Amboseli groups concerning specific points — rank reversals, menstrual cycles — with observations on intermediate days by R. Mututua, A. Samuels, and S. Sloane. We supplemented our own observations on EC with a second set of observations on coalitions from a study on consortship takeovers by G. Eggink and R. Kleinjans (unpublished data), gathered during May–November 1984 on 69 days not coinciding with our own observations.

Coalition, Alliance, Partnership

A *coalition* is an interaction between two individuals that each directed at least one threat or attack element toward the same opponent synchronously or ≤ 5 sec after each other. We excluded the (rare) mass chases of five or more individuals on a single opponent from the analysis. Within the context of a single conflict, we counted a particular coalition against a particular opponent only once. *Coalition partners* are participants in a coalition. Their opponent is a *target*. *Alliance* and *ally* refer to pairs that form coalitions exceptionally often. We use the term *partnership* more loosely for relationships in which coalitions regularly occur but not necessarily frequently.

Dominance and Rank

We inferred the formal dominance relationship (de Waal, 1987) between two animals on the basis of behavior during conflicts that were least

Table II. Subjects and Observation Time

Male	Birth	In group until	Residence (days) ^a	Observation time (hr) ^b	N focal samples	Remarks
Hooks group (Amboseli Natl. Park: 1 Dec. 1981–30 Nov. 1982)						
H1 ^c	24 Dec 1974		-158	362	58	=A9
H2			-81	530	77	
H3			61	671	98	
H4			219	671	100	
H5	±1969		523	671	99	Born in Alto
H6			538	671	101	
H7			±1461	671	95	
H8		26 Apr.	>1522	268	41	=A8
H9	±1974	1 May	Natal	268	43	Emigrated
H10	± 1975		Natal	671	101	
Alto's group (Amboseli Natl. Park: 1 Dec. 1981–30 Nov. 1982)						
A1			-310	134	9	
A2			423	785	65	
A3			443	785	67	
A4			1303	785	67	
A5			358	785	65	
A6			1027	785	67	
A7			1094	785	67	
A8		7 Nov.	-204	296	27	=H8
A9	24 Dec. 1974	27 Feb.	Natal	209	16	=H1
A10	1 Jan. 1975		Natal	785	66	
A11	18 Aug. 1975		Natal	785	67	
A12	15 Oct. 1975		Natal	785	69	

Eburru Cliffs group (Gilgil: 25 Mar.-25 Nov. 1984)					
E1	±June 1976	Natal	751 (637)	35	
E2		-9	570 (584)	26	
E3		1411	648 (609)	34	
E4	23 Apr. 1976	-28	568 (562)	30	Born in PHG ^d
E5	<1976	Natal	751 (636)	34	
E6	<1976	Natal	289 (132)	16	Emigrated
E7		-107	372 (380)	18	
E8	<1976	Natal	621 (601)	32	Made excursions
E9	~1977	-28	64 (0)	2	From/to PHG
E10	<1975	Natal?	385 (270)	18	Emigrated or died
E11		±2731	722 (616)	32	
E12		-13	627 (566)	28	
E13	Jan. 1977	Natal	751 (637)	32	
E14	<1976	Natal	631 (628)	26	Made excursions
E15	<1975	Natal?	741 (626)	34	
E16	25 Apr.	1507	95 (0)	6	Probably died
E17	14 May	666	161 (0)	10	Emigrated or died
E18	± Jan. 1970	2716	709 (508)	34	Born in PHG
E19	1 Mar. 1977	Natal	751 (637)	34	
E20	7 Apr. 1977	-114	347 (385)	26	Born in PHG

^a Time elapsed between immigration and start of study; negative figures are immigrations during the study (days after start).

^b Observation time for EC; in parentheses, observation time by G. Egink and H. Kleinjans.

^c **Boldface:** male transferred during study period.

^d PHG: Pumphouse group, the main study group at Gilgil.

likely to be influenced by other group members. We used all dyadic conflicts and the starting dyads of polyadic conflicts. In a preliminary study we found six submissive elements (*lean-aside/flinch*, *jump back*, *tail-up*, *grimace*, *gecker*, and *scream*) that occurred frequently enough to be analyzed to be highly consistent with each other in appointing the same individual as *loser*. A male was considered subordinate to another male when he showed at least one of these six submissive elements, while his opponent showed none of them.

We considered relationships to be undecided over periods between conflicts in which we observed unidirectional submission in opposite directions, or in periods between a conflict with bidirectional submission and any other type of conflict. We considered a relationship undecided if we did not witness submission by either male for more than a month.

We did not analyze the relationship between coalition formation and rank position independent of the identity of the male that occupied each rank slot, since that would have blurred the influence of individuality and of continuity in relationships. According to this philosophy each male is assumed to have behaved in a manner typical for the rank that he had during the period in which he formed the majority of his coalitions. This rank is indicated in the individual code.

Corrections for Absence and Time in Consort

Unless stated otherwise, we corrected all data for absence. We calculated different correction factors for marginal totals and for individual cells of each data matrix and separately for total observation time, total time of focal samples, and total number of point samples. In some cases, indicated in the text, we have corrected data for *time in consort* in such a way that the resulting data on a relationship between two animals reflect a situation in which neither of them consorted with a female (Noë and Sluijter, 1990; Noë, 1992).

Statistical Tests

All our tests are nonparametric. When a specific, alternative hypothesis is formulated, the tests are one-tailed (Siegel and Castellan, 1988; Sokal and Rohlf, 1981). For matrix statistics we used the Kr test (Hemelrijk, 1990a, b; de Vries, 1993).

RESULTS

Rank Orders and Dominance Reversals

Stability of Agonistic Rank Orders

We illustrate rank, periods of undecided dominance and dominance reversals in the form of a diagram for the Amboseli groups HOOK and ALTO (Fig. 1). We observed one rank reversal in each group (H4/H5/H6 and A3/A4) early in the study. We observed few coalitions involving these males before the rank reversals, so we could use the rank occupied after the reversals for our analysis. The two natals A9 and A10 reversed rank with several immigrants, but were little involved in coalition formation. One rank reversal in ALTO involving four males (A5 through A8) occurred during the study and coincided with a change in the pattern of coalition formation (Noë, 1986). Therefore, the data on ALTO have been split into a period before and a period after the reversal for some analyses. Although the period after the reversal was much shorter than the period before the reversal, the number of coalitions is roughly the same.

The number of males in EC was so large and the observation conditions so problematic that we could not construct reliable dominance matrices for the periods between changes due to immigrations and dominance reversals. Therefore, we present a single dominance matrix (Fig. 2) that gives an overview over the whole observation period.

Rank as an Indicator of Fighting Ability

A number of facts about rank and dominance relationships are important for the interpretation of our results.

Our observations confirmed the rule that young, healthy immigrants (H1, H2, H3, A1, E2, E4, and E7) usually obtain a high rank shortly after their immigration. E7 originally ranked higher, but dropped in rank after being wounded by dogs. There is one exception: E20 fitted in the rank order directly below a 1 month older natal male (E19), although he was almost exactly the same age at immigration as the more successful male, H1. The long-term records of the Amboseli groups (courtesy J. Altmann, S. A. Altmann, and G. Hausfater) show that H4, H6, A2, and A4 also obtained rank 1 shortly after their immigration. An old, crippled male (A8 = H8) and an unknown immigrant with fully worn teeth (E12) achieved low rank after immigration.

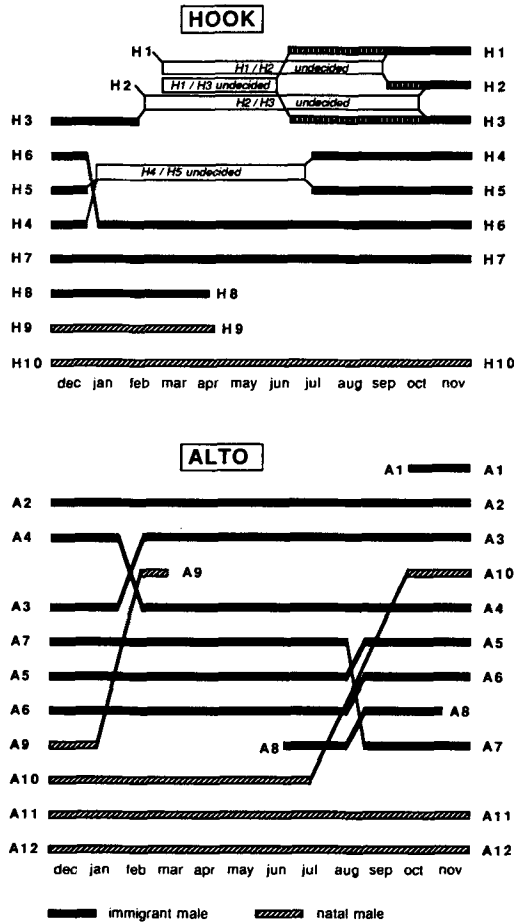


Fig. 1. Outline of the dominance relationships based on observations of dyadic interactions in the Amboseli groups between December 1, 1981, and November 30, 1982.

Natal males may climb rapidly in rank and become sexually active. Their dominance relationships with older immigrants resemble those of young newcomers (Strum, 1982), confirming the idea that rank is determined mainly by age. EC had seven such males, three of which became alpha males successively during our study.

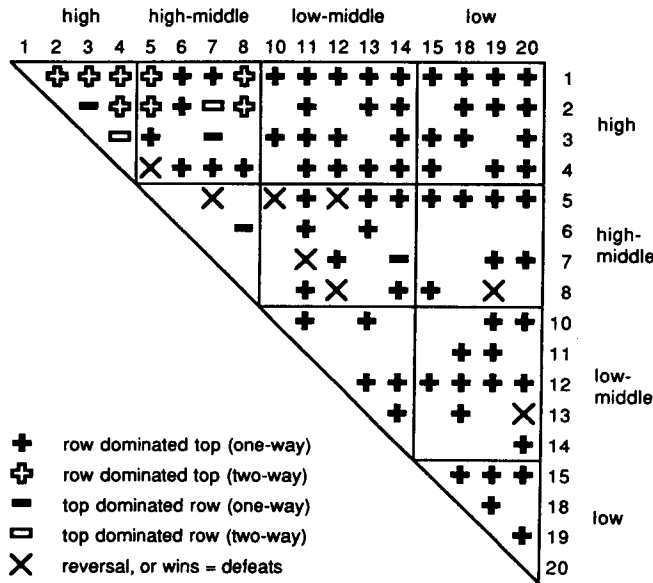


Fig. 2. Dominance matrix of EC based on observations on dyadic interactions between March 23 and November 25, 1984. Two-way relationship: Both males were seen to give submission during the observation period. Pairs for which no symbol is given: No conflicts were observed.

Some males have been assigned to different rank slots, but had virtually identical fighting ability, judging from the long periods of undecided dominance relationships and rank reversals. The most important examples are the three young immigrants in HOOK (H1, H2, and H3) and the males belonging to the high and high-middle subsets in EC. Such subsets of males should be considered to occupy a single fighting ability slot in the sense of the models presented by Noë (1992, 1994).

Coalitions and Alliances

Are Alliances Special Relationships?

The frequencies of coalitions for each pair of males are in Table III. One can ask whether the higher values represent the extreme values in a continuous distribution or the exceptional pairs in a discontinuous distribution. In the latter case, the use of the term alliance for these special relationships would be warranted. We compared the observed frequencies

(c) Coalitions EC (total number observed: 175)^b

	E1	E2	E3	E4	E5	E6	E7	E8	E10	E11	E12	E13	E14	E15	E18	E19	E20	Total per male	(Corrected for absence)
E1	—	2	1	1	19	—	—	—	1	1	—	1	—	1	—	2	—	28	
E2		4	1	1	2	1	2	1	—	—	1	—	—	—	—	—	1	13	(15.6)
E3			12	14	2	2	2	6	1	2	1	—	2	1	1	2	1	53	(58.5)
E4				9	1	—	1	5	—	1	1	2	—	1	—	1	1	36	(44.2)
E5					2	2	2	5	1	1	7	3	2	4	3	3	—	77	
E6					—	—	—	5	—	—	—	—	—	1	1	—	—	12	(39.6)
E7						—	—	2	—	—	1	—	—	—	1	1	—	12	(22.1)
E8							1	—	1	1	4	—	—	—	1	—	—	31	(35.2)
E10							—	—	—	—	—	2	—	—	1	—	—	7	(17.0)
E11								—	—	—	1	1	—	2	—	—	—	9	
E12												—	—	2	—	1	—	19	(22.1)
E13												—	—	—	—	—	—	10	
E14													—	—	—	—	—	4	(4.4)
E15														—	—	—	—	12	
E18															—	1	1	10	(11.4)
E19																2	—	13	
E20																—	—	4	(7.6)

^a Observed frequencies of coalitions per pair. **Boldface:** alliances. X: structural (a priori) zero.

^b Males not included: E9, E16, and E17 (<200 hr of observation time).

Table IV. Goodness of Fit Between Observed Distributions of Coalitions and a Poisson Distribution

Group	<i>N</i> pairs	Mean	Variance	χ^2	df ^a	<i>p</i>
HOOK	43	4.95	109.38	88.27	4	<0.001
ALTO	64	3.72	36.74	116.11	5	<0.001
ALTO						
Before ^b	54	1.94	13.60	49.18	3	<0.001
After ^b	55	1.96	10.03	42.62	3	<0.001
EC	134	1.73	9.82	101.40	3	<0.001

^a Several classes lumped in order to form classes with expected frequencies ≥ 5 .

^b Before and after a major rank reversal.

to a Poisson distribution. Table IV shows the results of goodness-of-fit tests. All observed distributions show a contagious pattern, i.e., there are more pairs than expected with very low frequencies as well as more pairs with very high frequencies. Therefore, a distinction between alliances and normal pairs seems meaningful. We used $\alpha = 0.05$ divided by the total number of pairs in the group as a formal cutoff point to distinguish alliances from other pairs. In this way, chance hits due to the large number of pairs in a group are unlikely, and the cut-off points for groups of different sizes are equivalent. We list the alliances thus defined in Table V.

Frequency Distribution of Coalition Formation per Male

The marginal totals in Table III, corrected for absence, indicate the relative participation of individual males in coalition formation. Figure 3 shows the pattern of deviation from the expected value under the assumption that all males form coalitions equally often in the form of standardized residuals ($O - E/\sqrt{E}$). We analyzed the data for ALTO separately for the periods before and after a major change in the rank order.

Male Attributes: Rank and Period of Residence

Table VI gives the correlations among rank, period of residence, and coalition frequencies for all immigrant males of the Amboseli groups present at the end of the study. We expected the frequency of coalition formation to be higher for males of lower rank (i.e., positively correlated

Table V. Exceptional Values of Frequencies of Coalition Formation Compared to a Poisson Distribution

	Critical value	Alliance	Frequency observed	Status of allies ^a
HOOK	14	H5-H6	55	R-R
		H5-H7	23	R-R
		H6-H7	37	R-R
		H6-H10	18	R-N
ALTO	13	A4-A5	27	R-R
		A4-A7	31	R-R
		A5-A6	16	R-R
		A5-A7	16	R-R
		A5-A8 ^b	13.3	R-I
Before	9	A4-A5	13	R-R
		A4-A7	22	R-R
		A5-A7	9	R-R
After	9	A4-A5	14	R-R
		A4-A7	9	R-R
		A5-A6	14	R-R
EC	9	E1-E5	19	N-N
		E3-E4	13.7	R-I
		E3-E5	15.0	R-N
		E4-E5	9.7	I-N
		E6-E8	16.0	N-N

^a R, nonnatal resident (immigration ≥ 1 year before start of observations); N, natal resident; I, immigrant (immigration during observation period).

^b Pair omitted from analyses, because the observed value was barely higher than the critical value and the correction factor for absence was high (2.7).

with rank number) and for males with longer periods of residence. We also used the partial rank correlation technique to test for a correlation between coalition frequency and either parameter. There were too many uncertainties in the rank order of EC to conduct similar tests.

Attributes of Relationships: Shared Experience, Affinity, Rank Sum, and Rank Distance

We used matrix statistics (Hemelrijk, 1990a, b; de Vries, 1993) — one-tailed Kr test with 2000 permutations — to test the correlation between some parameters of the quality of male-male relationships and the frequency of coalitions observed in those pairs. We conducted the tests for the immigrant males of the two Amboseli groups. We did not use the data on EC because period of residence and the rank were uncertain for several individuals. Table VII lists all correlations for HOOK and ALTO.

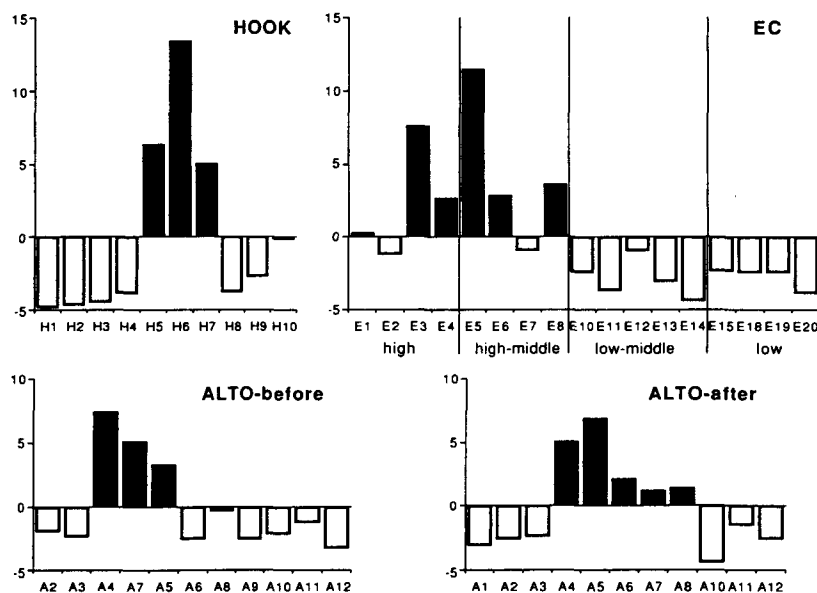


Fig. 3. Deviations from the expected frequencies of coalition formation per male. The expected frequency for each male is equal to the average number of coalitions formed in his group. Given are the standardized residuals ($O - E/\sqrt{E}$). Positive residuals (black bars) indicate higher-than-expected frequencies. The data for ALTO are given for the periods before and after a major rank reversal. Note the difference in the rank orders for ALTO: A9 emigrated, A1 immigrated, and A7 dropped in rank. For the rank order of EC, see Fig. 2.

Apart from the frequency of coalitions formed per pair (COAL), the following parameters have been included: (1) Proximity ≤ 2 m (PROX 2m) and (2) proximity ≤ 5 m (PROX 5m) are assumed to be measures of affinity. (3) Sexual greetings (SEX-GREET) are likely to be an indication of friendly relationships, but also occur in a variety of other contexts, e.g., between partners before the start of a coalition and between animals with an ambiguous dominance relationship (Smuts and Watanabe, 1990; Colmenares, 1990, 1991; own observations). (4) The period of shared residence (SHARED RESD) is a measure of familiarity. (5) RANK SUM is the sum of the ranks of the two members of a pair. A positive correlation of COAL with this parameter means that coalitions are formed by lower rather than higher ranking males. (6) The parameter RANK DIST has a higher value for pairs with shorter rank distances (formula: $N_{\text{males}} - \text{rank distance}$). (7) RANK SUM + DIST is a simple addition of the values for parameters 5

and 6. Other obvious arithmetical manipulations to form a combined parameter — $(\text{RANK SUM} \cdot \text{DIST})$ and $(\text{RANK SUM} + 2\text{DIST})$ — give virtually identical results. By using this parameter, one can test the prediction that coalitions are primarily formed by males that are both relatively weak. This approximates a prediction based on a model of Noë (1994), albeit that the model predicts the highest coalition frequencies for adjacently ranking males of middle rank, rather than of low rank.

The reader might have expected us to use grooming as a parameter, as is often done in primate studies, but it is extremely rare among adult male baboons and only occurs in very tense situations.

Familiarity and Friendship

Do the alliances, as defined under Coalitions and Alliances, differ from other pairs of males with respect to affiliative behaviors or familiarity? We consider two additional signs of a good relationship here: a low frequency of agonistic interactions within a pair and a low frequency of coalitions with other adult males against the other member of the pair. We ignored sexual greetings vis-à-vis the results of the matrix tests. In almost all cases, the number of allies per male is too low to conduct a Mann-Whitney *U* test to compare allies with nonallies. Therefore, we limited ourselves to simple inspection of the data.

Shared Residence in the Study Group

The immigrants that formed alliances in HOOK (H5, H6, and H7) had all been in the group >1 year. A4, A6, and A7 had been in ALTO >2 years, but A5, a male that had probably migrated more than once, had been in the group <1 year at the end of the study period. In EC newcomer E4 was involved in two of five alliances. E1 (member of one alliance), E5 (three alliances), and E6 and E8 (in an alliance together) were all natal members. Only E3 (two alliances) was a long-term resident. The other four long-term residents were not members of any alliance.

Proximity

We ranked the 28 pairs of immigrant males in each of the two Amboseli groups according to their score on proximity ≤ 2 m, proximity ≤ 5 m, and the number of coalitions formed. Table VIII shows that the allies did not rank high for proximity ≤ 2 m, but in both groups, the pairs with the highest number of coalitions were also the pairs with the highest score in

proximity ≤ 5 m. There is no corresponding pattern for the rest of the pairs. In two of five alliances in EC, the allies were each other's most preferred adult male neighbors. Otherwise, we noted no obvious relationship.

Agonistic Interactions

We examined the relationship between alliance formation and frequency of agonistic interaction during the focal male samples. In general, all middle- and low-ranking males — and not only allies — had low frequencies of agonistic conflicts among themselves. Some alliances (H5–H6, A4–A7) had low frequencies of interaction vis-à-vis their relatively frequent proximity. H6 and H7 had conflicts exceptionally often, however, without having an exceptionally high frequency of close proximity. Interestingly, the latter males were “played off” against each other by H5 in the process of alliance formation (Noë, 1990).

Coalitions Contra Allies

Refraining from forming coalitions with other adult males against the ally was not typical for alliances in general, but was found in two exceptional cases. In both ALTO and HOOK we observed a triad of males that formed alliances among each other [A4–A5–A7 and H5–H6–H7 (Noë, 1986, 1990)]. The highest-ranking males in these triads (A4 and H5) never formed coalitions with other adult males against their allies, except with one of the allies against the other ally. H5 always sided with H6 when he interfered in conflicts between his two allies. A4 consistently choose pro A7 and contra A5 before A7 dropped in rank but reversed his preference thereafter (Noë, 1986). The lower-ranking members of the triads never formed coalitions against A4 or H5, with the exception of one coalition in which H6 briefly turned against H5. Thus, the members of two alliances did not form coalitions with other adult males against their ally. They regularly supported females and immatures against their ally.

DISCUSSION

Coalition Formation and Attributes of Individuals

Two attributes of individual males play a role in our hypotheses: age — estimated by the period of residence — and fighting ability — estimated by rank. Our data confirm findings in other studies (Noë, 1992) that young

Table VI. Correlations Among Rank, Period of Residence, and Coalition Frequencies^a

	T	p
HOOK (<i>n</i> = 7) ^b		
Kendall's rank test		
Rank-Residence	1	<0.0001
Rank-Coalitions	0.619	0.035
Residence-Coalitions	0.619	0.035
Kendall's partial rank test		
Not relevant in view of the perfect Rank-Residence correlation		
ALTO (<i>N</i> = 7) ^b		
Kendall's rank test		
Rank-Residence	0.524	0.068
Rank-Coalitions	0.333	>0.10
Residence-Coalitions	0.429	>0.10
Kendall's partial rank test		
Coalition-Rank•Residence	0.140	>0.10
Coalition-Residence•Rank	0.299	>0.10

^a One-tailed tests.^b Immigrant males present at the end of the study.

adult newcomers usually gain high rank and that rank and period of residence of immigrant males are closely correlated. These findings are consistent with the idea that rank depends on fighting ability, which, in turn, depends on age according to a bell-shaped function. Due to the strong correlation between rank and the period of residence, we could not decide on the basis of simple rank correlation tests whether fighting ability (estimated by rank) or age (estimated by period of residence) is more likely to be an important male attribute in coalition formation (Table VI).

Coalition Formation and Attributes of Relationships

Three of our hypotheses are based on attributes of male pairs: familiarity, measured by the common period of residence, friendship, measured by proximity and affiliative behavior, and combined fighting ability, measured by the sum of ranks. The only statistical technique available for the analysis of such data is matrix statistics (Hemelrijk, 1990a, b; de Vries, 1993). Before we evaluate our results we will discuss some problems with this technique.

We found that some males form coalitions exceptionally often. The presence of such exceptional relationships makes the interpretation of the results

of matrix tests precarious, since the assumption of a continuous distribution is violated. This may give rise to two types of error. First, there is a risk of not finding relevant differences in the quality of the relationship between allies, on the one hand, and non-allies, on the other hand. This happens if the data on the few alliances are swamped, because no consistent correlation between two parameters exists within the large mass of non-alliances. Second, a strong correlation in a few pairs may lead to a significant result and therefore to the erroneous conclusion that the correlation holds for the whole group. To illustrate this problem, we constructed two 8×8 matrices as used in our tests, but with random numbers instead of observational data. We then systematically replaced the figures for some pairs with figures that showed rank correlation (e.g., 110, 120, 130 in one matrix and 210, 220, 230 in the corresponding cells in the other matrix) and conducted the same Kr tests as used in Table VII. This resulted in the following p values: four manipulated pairs, 0.064; five pairs, 0.035; and six pairs, 0.014. Thus, if five pairs would frequently form coalitions and often be in each others vicinity as well, one could erroneously conclude that coalition formation and proximity correlate over all 28 pairs. However, the conclusion may hold only for those five exceptional pairs. For the same reason one cannot use matrix statistics to show the existence of reciprocity at the group level, as was done by de Waal and Luttrell (1988) and Hemelrijk (1990b), for groups containing exceptional pairs like our alliances.

While chance hits are possible among the 50 correlations that we calculated, the results of the matrix tests have to be handled with care. We found only two correlations to be significant in both HOOK and ALTO: between the coalition formation and proximity ≤ 2 m and between coalition formation and a variable that combined the rank distance and the rank sum of a pair. The latter result is due to a strong correlation with the rank distance in HOOK and with the rank sum in ALTO. Other significant correlations point to a general underlying relationship between all parameters, except sexual greetings. The results strengthen the evidence for both the friendship hypothesis and the fighting-ability hypothesis. The impression from the data on HOOK that common experience (familiarity) plays a role could be due to the strong correlation in this group of the variable, shared residence, with both the combined rank sum and distance measure and proximity ≤ 2 m.

Evaluation of the Four Hypotheses

Experience and Familiarity

The experience and familiarity hypotheses are not supported by our data. We found no evidence for an increase with age in the number of

Table VII. Matrix Statistics to Test Correlations on the Level of Male-Male Relationships^a

Table VIII. Position of the Alliances in the Amboseli Groups in the Rank Orders for Coalition Frequency and Two Proximity Measures^a

Alliance	Coalitions	Proximity ≤ 2 m	Proximity ≤ 5 m
HOOK			
H5-H6	1	11	1
H5-H7	2	13	8
H6-H7	3	3	6
ALTO			
A4-A7	1	16	1
A4-A5	2	19-20	17-28 ^b
A5-A6	3-4	3	13-15
A5-A7	3-4	5	4

^a Position in rank order of 28 pairs of immigrant males. Frequencies have been ranked in descending order (1 is highest frequency).

^b One of 12 zero scores.

coalitions formed for males past their prime. Instead, we found a bell-shaped relationship with age in HOOK and ALTO. In EC the younger, not the older, males frequently formed coalitions. Four of six males involved in alliance formation were natal males of known age and they belonged to the youngest (7 to 8-year-old) age group among the adult males. Experience does not decrease with age. Thus, the relationship must be explained by correlation with a factor, like fighting ability, that produces a bell-shaped correlation with age. The fact that alliances can be formed by newcomers (Bercovitch, 1988; this study) suggests that a long-lasting relationship is not a prerequisite for the formation of alliances.

Friendship

Like Collins (1981), we found that allies are not necessarily often in each other's proximity. The significant correlation between coalition formation and proximity ≤ 2 m in the matrix tests is not due to the alliances. Only the two strongest alliances, H5-H6 and A4-A7 (the latter only in the first half of the observation period) had high proximity scores, but at the ≤ 5 -m level, not at the ≤ 2 -m level (Table VIII). It is remarkable that, in our matrix tests, we found no significant correlation between the independently sampled proximity measures ≤ 2 m and ≤ 5 m. This could point to a crucial difference in the level of tolerance that is measured by the two distance parameters.

For the majority of alliances, we could not find other evidence supporting the friendship hypothesis. However, the members of two pairs that were often

in close proximity (≤ 5 m; Table VIII) — H5–H6 and A4–A7 — also had few agonistic conflicts and formed virtually no coalitions with other adult males against each other. In EC, the members of one alliance also had an exceptionally strong affiliative bond (Smuts, 1985, p. 148). This alliance (AA and BZ; the latter is our E11) had been observed in 1977, still existed when we started our observations in October 1983, and ended when AA was shot in February 1984.

Fighting Ability

A common pattern for the three study groups is apparent from the data in Table III and Fig. 3: The highest-ranking males formed few coalitions, a group of males ranking directly below them formed coalitions frequently, and the lowest-ranking tail of the adult male subgroup again was little involved in coalition formation. To appreciate the resemblance in patterns for the different groups, notably HOOK and ALTO, one must recall that the hypothesis tested is based on fighting ability and that rank is used as its substitute. Males with virtually identical fighting abilities — H1, H2, and H3 — would have occupied a single slot if fighting ability had been used instead of rank.

A shift in rank due to the arrival of a new high-ranking male should change little in the fighting abilities of the resident males and thus the pattern of coalition formation, although the middle-ranking males may have a new target. A rank reversal, however, is a clear indication of a change in fighting abilities, and according to the fighting ability hypothesis, the pattern should change. After immigrations at the top (H1 and H2 in HOOK, A1 in ALTO) the group of coalition-forming males simply shifted down-rank. Concurrently with the rank reversal in ALTO, however, the pattern of coalition formation changed considerably, e.g., the changes for A6 and A7.

A similar bell-shaped distribution was observed by Rasmussen (1980) for a larger group with 13–15 adult males, by Collins (1981) in a medium-sized group with 8 adult males, and by Bercovitch (1988) in a group in which the number of adult males varied considerably (Bercovitch, 1986). On the basis of the consistency of this pattern, we agree with Bercovitch (1988) that relative fighting ability forms the key to alliance formation. We think that the explanation for the low frequencies of coalitions among high-ranking males is different from the explanation for the low frequencies in low-ranking males. As we showed earlier (Noë and Sluijter, 1990), it does not pay for high-ranking males to form coalitions and to share resources, since they can reach their goals single-handedly. We assume that males of low fighting ability would have most to gain from coalition formation. The highest number of coalitions would also be found among these males, if experience and familiarity would play a crucial role,

since they are usually relatively old and long-standing in the group. We speculate that they, nevertheless, participate in few coalitions, because they are not attractive as partners due to their weakness. We used these assumptions as a basis for a post hoc descriptive model, which shows that the observed pattern of coalition formation among male baboons can be generated on the basis of the parameter fighting ability alone (Noë, 1992, 1994).

The Causal Arrow Between Alliance Formation and Proximity

In two cases the members of an alliance were frequently in each other's proximity. What came first, the alliance or the frequent close proximity? Several facts speak for a causal arrow from alliance formation to proximity. These alliances are the only 2 of 13 alliances with such high scores for proximity ≤ 5 m. However, when A7 dropped in rank, A4 replaced him with A5, a male with which he was much less familiar and with which he was not often in close contact (Noë, 1986). There are alternative explanations for frequent proximity of the allies that do not necessarily imply an affiliative relationship.

First, the frequent close proximity can be a direct consequence of the tactics used. When an alliance is used in defense against attacks of high-ranking males, the allies have to be near each other whenever attacks might be expected. Offensive use of alliances can also force the allies to remain together for a much longer time than the actual coalitions themselves last. Coalition partners usually trailed a consort pair, occasionally for more than an hour, before they attacked the consorting male.

Second, a high proximity score can be a by-product of frequent proximity to the same group members. For example, H5 and H6 had high overall proximity scores, especially with immatures (Noë and Sluijter, 1990), and frequently had the same immatures as neighbors (Kendall partial r 0.43, $p < 0.01$; proximity scores of both males with 18 immatures with total proximity score of each immature with all adult males partialled out). Thus, opportunistic partnership rather than friendship would be the appropriate anthropomorphic term for these two alliances.

Is the Pattern of Coalition Formation Due to "Dependent Rank"?

Most alliances were formed by rank-neighbors. This phenomenon, which was also found by Collins (1981), Smuts (1985), and Bercovitch (1988), could be a result of alliance formation, rather than providing

evidence that alliances are more readily formed by close neighbors. The rank of allies could have been determined, to a large extent by the fact that they can rely on the support of their allies. Kawai (1958) labeled this phenomenon dependent rank. According to this explanation, the drop in rank of A7 would have been due to a change in alliance structure, not the other way around. We assert, however, that the fact that coalitions are often formed by rank-neighbors cannot be explained by a dependent rank argument alone. First, our rank orders are based on what Kawai called basic rank, i.e., on dyadic interactions in which direct influence of third individuals was unlikely. Thus, the pattern could be explained only if the influence of the alliances would be so strong that a male could maintain his dominance status in the temporary absence of his ally. Second, several lower-ranking allies did not obtain a rank directly below their higher ranking ally (e.g., H6-H10, E1-E5). Therefore, we consider it more plausible that the clumping, as well as the position of the clump in the dominance rank order, is explained by the fact that males with a specific range of relative fighting abilities tend to form coalitions. The model presented in Noë (1994) provides further support for this assertion.

CONCLUSION

Male baboons neither have to be very experienced nor have to know each other very long to be able to form coalitions. The formation of alliances among adult male baboons is determined mainly by relative fighting ability and, to a much lesser extent, by the affiliative quality of relationships. Some allies had a more affiliative relationship than is usually observed among adult males, but we have the impression that such a friendship develops between allies as a mechanism to cement the alliance, rather than being a prerequisite for alliance formation.

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