

DEMOGRAPHY AND BEHAVIOR OF ONE-MALE GROUPS OF  
YELLOW BABOONS (PAPIO CYNOCEPHALUS)

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## Abstract

Groups of baboons with only one adult male are considered typical only of the arid habitat hamadryas species (Papio hamadryas). However, in 1971-72, 20% of the yellow baboons (Papio cynocephalus) in the Amboseli National Park, Kenya, lived in groups with only one adult male. In recent years the Amboseli ecosystem has become increasingly xerophytic; this study was undertaken to determine if the formation of one-male groups was an adaptive response to Amboseli's changing ecology. These one-male groups also presented an opportunity to investigate the role of adult males in group organization.

Both multi-male and one-male groups declined over the fourteen month study period; however, one-male groups declined at a significantly greater rate than did multi-male groups, primarily due to higher mortality. Thus, one-male groups were not better adapted than multi-male groups to the dryer ecological conditions, and were probably merely the remnants of former multi-male groups.

The overall rates of social interaction for all age-sex classes were lower in one-male groups than in the multi-male group for which comparable information was available. However, when by chance a second, and then a third, adult male temporarily joined a one-male group, the rates of social interaction among all classes of individuals

decreased, even though the number of potential social partners had increased. Thus, rates of social interaction were not determined by group size alone, but also were dependent upon the specific age-sex and individual composition of the group. The role of the single adult male was not as specialized as it has been described for males in multi-male groups; adult females as well as males defended the group against predators and the adult male maintained no fixed position in group progressions.

Comparing hamadryas and yellow baboon one-male groups, this study pointed out that P. hamadryas evolved in its desert habitat over many generations while the one-male groups of yellow baboons in Amboseli were a recent, possibly ephemeral result of a declining baboon population distribution. In sum, one-male units of hamadryas baboons were uniquely adapted to their xerophytic habitat; one-male groups of yellow baboons were not.

## I. INTRODUCTION

Savannah baboons of the genus Papio (P. cynocephalus, P. anubis and P. ursinus) generally live in groups of about 30 individuals, including several adult males, about twice as many adult females, and subadults and juveniles of both sexes ( DeVore and Hall, 1965; Hill, 1967). Baboon groups composed of one or sometimes two adult males, several adult females and their young, are considered typical only of the arid-living hamadryas baboon (P. hamadryas) (Kummer, 1968), although one-male groups occasionally have been reported in each of the savannah species ( DeVore and Hall, 1965; Altmann and Altmann, 1970; Bolwig, 1959). The other species in the genus Papio, the guinea baboon (P. papio) exhibits group size and organization intermediate between that of hamadryas and savannah baboons (Boese, 1973).

This report describes demographic and behavioral characteristics of one-male groups of yellow baboons (P. cynocephalus) in the Amboseli National Park, Kenya. In 1971 about 20% of the Amboseli savannah baboon population were living in three groups, each including less than 20 members and only one adult male.

Several authors (e.g., Altmann, 1965; Crook, 1970; Goss-Custard et al., 1972; Washburn and DeVore, 1961) have speculated on the ecological and adaptive significance

of the particular age-sex composition and group size of savannah baboons. As an example of this significance, previous descriptions of savannah baboon behavior have emphasized the importance of cooperation between adult males both in influencing intragroup behavior and in defense of the group from predators. The presence of only one adult male doubtless affects group organization and the behavior of all classes of individuals. Based on comparative information for multi-male groups, several questions about one-male groups immediately come to mind: Does the one adult male continue to defend his group from predators or do adult females and juveniles participate in predator defense, or does the entire group flee without overt defense? Similarly, a strict progression order and protective spatial distribution of adult males is thought to be an important part of the adaptation of savannah baboon groups for life on the ground (Rhine, 1975; Rhine and Owens, 1972). Where does a lone adult male position himself during progressions? Aggression by adult males in savannah baboon groups is most frequently directed against other adult males (Hausfater, 1975). With whom does a lone adult male interact, agonistically or otherwise, and with what frequency? What is the effect on rates of social interaction of a second adult male joining a previously one-male group? Finally, how do rates of social interaction, dominance relationships and other aspects of social organization in one-male groups compare to those of multi-male groups?

These one-male groups are of ecological as well as behavioral interest. In a socioecology model relating group size to habitat, Crook (1970) hypothesized that one-male groups of primates are an adaptation to a sparse resource distribution and low predator density. These conditions often are found in arid regions, although Aldrich-Blake (1970) has suggested that some tropical rainforest primate species effectively may be living under these same ecological conditions. It is argued that smaller, wider-ranging groups are more efficient than larger groups in exploiting such sparse resources, while the low density of predators results in a single large adult male and many smaller females as the optimal distribution of biomass within these small foraging units. In essence, none of the scarce resources would be "wasted" on large non-reproducing adult males who have been made unnecessary by low predator density. The consequences of these hypotheses for mating systems and sexual selection have been explored by Goss-Custard et al. (1972), while Wilson (1968) has described the conditions necessary for optimal distribution of biomass to take place as a result of group selection, as is implied by some of the above arguments.

Since the initial study of Amboseli baboons in 1963-64 by Altmann and Altmann (1970), the Amboseli basin has undergone major ecological changes. Specifically, a rise in the water table has coalesced alkaline deposits and salts



in the upper soil layers causing a die-off of yellow-barked acacia trees, Acacia xanthophloea, and associated understory (primarily Azima tetracantha and Salvadora persica) (Western and Van Praet, 1973). Water is plentiful at localized waterholes.

The densities of baboons, vervets (Struhsaker, 1973), several game species and their predators (Western, 1973), have decreased markedly in the Amboseli basin, presumably in relation to the changes in vegetation cover and water table. The die-off of trees also has decreased the number of sleeping groves for baboons, and frequently several groups share one sleeping site at night. In general, Amboseli has changed from a habitat considered typical for savannah baboons to a habitat for which a socioecology model predicted the presence of one-male groups.

Previous "tests" of the socioecology model of group size and sex ratio in the genus Papio have been correlational. In essence, these tests have shown that the mean (or "normative") group size and ratio of adult males to females for one species in an arid environment is smaller than the mean group size and number of males per female for the same or a closely related species in less arid environments. For example, arid-living hamadryas baboons forage in groups of a smaller mean size than do yellow baboons living in the savannah. A critical evaluation of this method has recently been published by

Altmann (1974). However, a second method of testing the above hypothesis is available. If one particular group size or sex ratio is the adaptive optimum for a particular environment (e.g., small, one-male units in an arid environment), groups which differ from this optimum should suffer a decreased reproductive rate, increased death rate, or both (Altmann and Altmann, 1970). The analyses that follow, (1) compare rates of natality and mortality for one-male groups and multi-male groups living in the same environment, (2) describe dominance relations and general details of social organization within one-male groups, (3) compare rates of social interaction in one-male groups with multi-male groups, (4) analyze changes in rates of social interaction within a small group that changed from a one-male group to a two-male group, to a three-male group, and then back again, and (5) examine the position of the one adult male in progressions. Finally, (6) behavior in one-male groups of yellow baboons and hamadryas baboons will be compared and some speculations on the origin of hamadryas social organization presented.

## II. METHODS

### Study Site and Population

The study site and ecology of Amboseli baboons have been described by Altmann and Altmann (1970). Briefly, Amboseli is a region of short grass savannah. In the center of the park, swamps and permanent waterholes fed by underground streams from Mt. Kilimanjaro provide year round water for baboons and many other species of animals.

### Demographic Data and Observation Times

When this study began in August 1971, there were about 200 baboons in seven groups living in the 34 km<sup>2</sup> study area. Three of these seven groups were censused monthly through mid-September 1972, when the study ended; a fourth group, Kitirua South, visited the study area infrequently and consequently was censused only a few times. The remaining three groups - Alto's, High Tail's, and BTF - were censused on every day of observation, almost daily. In a census, individuals were grouped into the following six age-sex classes: Infant-1 (I1), newborn to six months, Infant-2 (I2), six months to one year, Juvenile-1 (J1), one to two years, Juvenile-2 (J2), two to four years, Subadult male (Sub), four to six years, Adult male (Ad♂), six years or more, and Adult female (Ad♀), four years or more (Altmann and Altmann, 1970).

Subsequent studies have shown that these age categories may underestimate the actual age by about two years (Altmann et al., 1975). Of the three main study groups, Alto's group was a multi-male group of about 32 individuals; Hight Tail's group and BTF group were smaller one-male groups of about 15 and 13 individuals, respectively. From November 1971 to mid-May 1972, High Tail's group was observed daily for 640.8 hours; from May through July 1972, observations were carried out on BTF group for an additional 400.0 hours. Primarily as part of another study (Hausfater, 1975), Alto's group also was observed for over 2500 hours throughout the study period. All individuals in each study group were individually identifiable on the basis of face, physique, and tail carriage. All observations were carried out from 0800 to 1800 hours daily while the group was followed in a field vehicle. Both census and social behavior data were entered on prepared data sheets or dictated into a tape recorder and later transcribed verbatim.

#### Behavioral Data

Data on rates of social behavior were collected by a focal animal sampling technique (J. Altmann, in press). In this technique, one individual was followed for a predetermined amount of time, usually thirty minutes; time during which the focal animal was out of view was

subtracted from the total sample length to obtain a time base for rate calculations. Six thirty minute focal animal samples were completed during each morning and six more during each afternoon of observation on the one-male groups. All individuals in these groups except infants (individuals less than six months of age) were sampled in a randomly determined order. In the multi-male group, focal samples of behavior were taken only on estrous females and adult and subadult males (Hausfater, 1975). These focal samples are believed to yield unbiased estimates of rates of social interaction and an unbiased sample of agonistic bout outcomes. Additional behavioral data were collected by an ad libitum technique, both when focal samples were not being taken and concurrently with focal samples. For the purposes of these analyses, it is assumed that ad libitum samples provided an unbiased sample of agonistic bout outcomes (but not of agonistic bout frequency), progression orders, and responses to predators. In fact it is very likely that all events of predation by baboons on other animals and of predation by other animals on baboons that occurred during observation periods were recorded in the ad libitum sample record.

Briefly, most social interactions fell into one of four broad categories: agonistic bouts, mountings (with or without ejaculation), presentation of the hindquarters,

and grooming. Descriptions of the behaviors included in these categories as well as further details of the sampling methods are given by Hausfater (1975). The last three categories taken together are referred to as "nonagonistic interactions" and all four categories combined are referred to as "total social interactions".

### III. RESULTS

#### Demographic Characteristics of One-Male Groups

In 1971-72, six baboon groups used the Amboseli study area daily while a seventh group, Kitirua South, entered the study area only infrequently. The sizes of the six frequently encountered groups at the beginning and end of the 12 month study are given in Table 1. Three of these six groups had from 30 to 70 members including several adult males. The other three groups had from 9 to 15 members and included only one adult male for some period of time. At the start of the study, the adult male: female sex ratio in one-male groups was 1:4 or 1:5 while the ratio for the multi-male groups was 1:1.5. All of the groups in the study area decreased in size, with an average net annual decline in group size of 10.9%. The continued decline in the Amboseli baboon population probably was somehow related to the continued deterioration of acacia trees and associated vegetation, but the exact nature of the relationship is still uncertain. Although the smaller one-male groups underwent a mean decline of 23.7%, the three large multi-male groups decline by only 9.7% and this difference was statistically significant ( $\text{Chi}^2$  two-sample test,  $X^2 = 9.38$ ,  $df = 2$ , .01 level). Thus, one-male groups declined at a faster rate than multi-male groups.

TABLE 1: Changes in group size between 1 August 1971  
and 1 August 1972.

<u>Group</u>	<u>August 1971</u>	<u>August 1972</u>	<u>Change</u>	<u>% Change</u>
Multi-Male Groups				
Stud	68	65	-3	- 4.4%
Hook	38	32	-6	-15.8%
Alto	36	35	-1	- 2.8%
One Male Groups				
High Tail	14	9	-5	-35.7%
BTF	13	11	-2	-15.4%
Limp	<u>15</u>	<u>12</u>	<u>-3</u>	<u>-20.0%</u>
Totals	184	164	-20	-10.9%



What specific demographic processes account for this significantly greater loss of individuals from the one-male groups? Groups change in size as a result of six processes: birth, death, emigration, immigration, fusion with another group, and fission into two smaller groups. Only the first four processes need to be considered here, although early in 1973 one of the three one-male groups actually did fuse with a larger multi-male group. The three main study groups were censused each morning of study. An individual present in one morning census, but missing from the census on the subsequent morning was scored as missing. If the missing individual later was seen as solitary or with another group, the score was changed to emigration; if the individual was never seen again, the score was changed to death. The actual cause of death was rarely determined since baboon remains were rapidly and completely consumed by the abundant predators and scavengers in the Amboseli National Park. Immigration was scored when an individual recorded in a morning census had not been recorded in the census of the previous morning. All births were recorded, as was the particular color of each adult female's paracallusal skin (PCS) (Altmann, 1970); consequently, no still-births or near-term aborted pregnancies went unobserved.

Table 2 presents data on changes in composition of three one-male groups and one multi-male group over the

12 month observation period: precise demographic data on the other multi-male groups were not available. Since emigrations equaled immigrations or differed only by one in all study groups, it is clear that differential emigration from one-male groups did not explain the greater decline in the size of these groups. Thus, the greater rate of decline of one-male groups compared to multi-male groups must be due to higher mortality, lower natality or both in the one-male groups.

Table 3 compares birth and death rates from the three one-male groups with Alto's group on the basis of data given in Table 2. Over a one year period there were five live births and one still-birth in the multi-male group, or a rate of one birth per female every 624.7 days. This figure matches closely the rate of 661.0 calculated for the Amboseli population in 1963-64 by Altmann and Altmann (1970) and the birth rate for forest-living anubis baboons (*P. anubis*) in Uganda (Rowell, 1966). In contrast, a total of seven infants were born to the 14 females in the one-male groups, or one birth per female every 724.6 days. This difference between the birth rate in one-male groups and the birth rate in multi-male groups is equivalent to a 14% decrease in fecundity for females living in one-male groups.

For all age-sex classes of individuals, the death rate was higher in one-male groups than in multi-male

TABLE 2: Summary of demographic processes between  
1 August 1971 and 1 September 1972.

<u>Group</u>	<u>Immigrations</u>	<u>Emigrations</u>	<u>Births</u>	<u>Deaths</u>
High Tail	7	7	2	7
BTF	4	5	3	3
Limp	?	?	2	5
Alto	17	16	6	7

TABLE 3: Death rates and birth rates between 1 August 1971 and 1 September 1972.

<u>Group</u>	<u>number of ♀ days</u>	<u>1 birth/ ♀ days</u>	<u>number of monkey days</u>	<u>1 death/ monkey days</u>
High Tail	1422	711.0	4751	678.7
BTF	1526	508.7	4001	1333.7
Limp	2124	1062.0	5089	1017.8
One-male groups combined	5072	724.6	13841	922.7
Alto	3745	624.7	10070	1438.6

groups (Table 3). One-male groups lost a member on average once every 923 days of observation (13,841 monkey days/15 deaths), while a multi-male group lost a member on average only once every 1,439 days, although the difference was not statistically significant.

Since natality was lower and mortality was substantially higher in one-male groups than in multi-male groups, one may conclude that the one-male groups reaped no survival advantage from being smaller foraging units in an arid environment and, in fact, actually were at a disadvantage compared to multi-male groups. These one-male groups probably resulted from the long term decline in the Amboseli baboon population and most likely represent the "tails" of a shifting population or group size distribution. Possibly these one-male groups were once multi-male groups, but have been reduced to small one-male units through the normal course of mortality in this population. Thus, the available evidence does not support the hypothesis that one-male groups in the Amboseli population are an adaptive response to the increasingly arid environment and declining predator density.

#### Behavioral Characteristics of One-Male Groups

##### Dominance Relationships

The criteria and definition of dominance used in this

work follows Hausfater (1975) and the reader is referred to that work for a more complete discussion. Briefly, dominance as the term is used here is a statement about the consistency, or agreement, of the outcome of successive agonistic bouts within pairs of individuals. If the outcomes of successive bouts within a pair of individuals are consistent, then the dominance relationship within that pair is inferred to be consistent as well. If, in addition, the relationships between pairs are transitive, then a linear dominance order or hierarchy results. An agonistic bout was defined as any sequence of behaviors that included at least one of the behavior patterns of aggression or submission in yellow baboons as listed in Hausfater (1975). An outcome or winner-loser determination was made in these bouts whenever one individual directed only submissive (and sometimes other non-aggressive) behaviors toward a second individual in response to only aggressive (or other non-submissive) behaviors from the second individual. Surprisingly, only 1% of all agonistic bouts (N=12) observed in High Tail's group and less than 1% of all agonistic bouts (N=3) observed in BTF group were undecided by these conservative criteria of dominance.

Tables 4 and 5 list the outcomes of all decided agonistic bouts recorded during observations on High Tail's group and BTF group, respectively. The first

number in each cell of these matrices gives the total number of outcomes within a pair of individuals recorded in ad libitum and focal animal samples combined; the second entry in each cell gives the number of outcomes within the pair recorded in focal animal samples alone. This table is read from left to right with those individuals listed in the column dominant to those in the rows. Dominance relationships in the one-male groups were in general linear and consistent. The two reversals, one in each group, were the result of a period of inconsistent dominance relations between two adult females in one case and between an adult female and juvenile female in the other. The adult male in each group was dominant to all adult females and juveniles; changes in the reproductive states of the adult females, including estrus or consortship with an adult male, did not result in any changes in their dominance relationships.

Tables 6 and 7 list the outcome of all agonistic bouts in High Tail group when a second male (Table 6) and when a third adult male (Table 7) temporarily immigrated into the group. Dominance relationships continued to be linear and consistent, and in particular, no change in adult female relationships occurred, although several females frequently groomed each of the additional males. Female dominance relationships in this small group apparently were independent of the females' relationships

TABLE 4: Dominance matrix for High Tail group with one adult male.

	High Tail	Jane	Este	Slinky	Crook	Big	Corrie	Toto	Handle	Brush	Plum	Grub	I of Big	I of Crook	I of Corrie	Sum
Ad ♂ High Tail *		9	14	4	18	3	8	5	2	7	1	2	1	1	1	76
		4	5	1	8	1	5	4	0	2	0	1	0	0	0	31
Ad ♀ Jane		*	10	5	15	7	6	2	5	10	5	2	0	0	0	67
			3	0	8	4	4	0	1	5	0	1	0	0	0	26
Ad ♀ Este			*	7	23	13	18	0	4	8	7	0	0	0	0	80
				3	18	6	11	0	2	5	5	0	0	0	0	50
J2 ♀ Slinky				*	11	2	9	2	7	7	6	2	0	0	0	46
					4	1	5	0	0	2	2	0	0	0	0	14
Ad ♀ Crook				*		6	12	2	2	11	7	0	0	0	0	40
					*	4	8	1	0	6	2	0	0	0	0	21
Ad ♀ BIG						*	10	0	0	7	3	0	0	0	0	20
							7	0	0	6	1	0	0	0	0	14
Ad ♀ Corrie							*	0	0	0	3	0	0	0	0	3
								0	0	0	3	0	0	0	0	3
J1 ♂ Toto								*	1	0	0	1	1	0	0	3
									0	0	0	0	0	0	0	0
J1 ♀ Handle									*	0	2	0	0	0	0	2
										0	0	0	0	0	0	0
J2 ♀ Brush										*	14	2	0	0	0	17
											3	0	0	0	0	3
J2 ♀ Plum											*	0	0	0	0	0
I2 ♂ Grub												*	0	0	0	0
													0	0	0	0
II ♂ I of Big													*	0	0	0
														0	0	0
II ♂ I of Crook														*	0	0
															0	0
II ♀ I of Corrie															*	0
																0

Total number of interactions:  
Interactions in focal samples only:



TABLE 5: Dominance matrix for BTF group with one adult male.

	K1	Nice	Joc	Kala	Muffet	Teeka	Bent	BTF	Romulus	Girl	Remus	I of BTF	I of Nice	Sum
Ad ♂ K1	*	8 4	25 8	21 8	18 5	1 0	22 10	6 1	4 1	17 12	3 0	0 0	0 0	124 49
Ad ♀ Nice		*	3 2	21 11	37 15	4 0	37 21	57 30	0 0	28 11	12 4	0 1	0 0	199 95
J2 ♂ Joc			*	1 0	31 16	0 0	15 10	10 6	18 6	28 11	24 7	0 0	0 0	127 56
Ad ♀ Kala				*	27 15	4 0	30 13	25 12	0 0	16 10	1 0	0 0	0 0	103 50
J2 ♀ Muffet					*	0 0	9 6	8 6	1 0	23 10	0 1	0 0	0 0	41 23
J2 ♀ Teeka						*	3 0	0 0	4 0	0 0	0 0	0 0	0 0	7 0
Ad ♀ Bent							*	46 24	0 0	5 4	1 0	0 0	0 0	53 28
Ad ♀ BTF								*	0 0	4 2	0 0	0 0	0 0	4 2
J1 ♂ Romulus									*	1 0	5 0	0 0	0 0	6 0
J1 ♀ Girl										*	0 0	0 0	0 0	0 0
J1 ♂ Remus											*	0 0	0 0	0 0
II ♂ I of BTF												*	0 0	0 0
II ♀ I of Nice													*	0 0

Total number of interactions: 664

Interactions in focal samples only: 303

TABLE 6: Dominance matrix for High Tail Group with two adult males.

	High Tail	Crest	Jane	Este	Slinky	Crook	Big	Corrie	Toto	Handle	Brush	Plum	Grub	I of Big	I of Crook	I of Corrie	Sum
Ad ♂ High Tail *		35	3	5	3	6	7	5	1	1	7	2	1	0	0	0	76
		4	0	3	0	3	3	0	0	0	2	1	0	0	0	0	16
Ad ♂ Crest		*	3	11	6	5	6	12	1	3	15	7	0	0	0	0	69
			1	3	1	1	2	6	0	0	7	2	0	0	0	0	23
Ad ♀ Jane			*	5	6	3	7	9	2	2	3	6	1	0	0	0	44
				3	2	2	4	4	0	0	2	3	0	0	0	0	20
Ad ♀ Este				*	6	4	11	25	0	4	13	6	0	0	0	2	71
					3	2	6	10	0	2	8	4	0	0	0	2	37
J2 ♀ Slinky					*	0	2	11	1	2	6	16	1	0	0	1	40
						0	1	8	0	1	1	9	1	0	0	0	21
Ad ♀ Crook						*	2	1	1	1	8	1	0	0	0	0	14
							1	0	0	0	5	0	0	0	0	0	6
Ad ♀ Big							*	17	0	0	8	4	0	0	0	0	29
								8	0	0	5	2	0	0	0	0	15
Ad ♀ Corrie								*	0	1	1	8	0	0	0	2	12
									0	0	0	3	0	0	0	1	4
J1 ♂ Toto									*	3	1	1	2	0	0	2	9
										0	0	0	0	0	0	0	0
J1 ♀ Handle										*	4	8	0	0	0	0	12
											3	3	0	0	0	0	6
J2 ♀ Brush											*	14	0	0	0	0	14
												6	0	0	0	0	6
J2 ♀ Plum												*	0	1	1	2	2
													0	0	0	0	0
I2 ♂ Grub													*	0	0	1	1
														0	0	0	0
II ♂ I of Big														0	0	0	0
														*	0	0	0
II ♂ I of Crook															0	0	0
															*	0	0
II ♀ I of Corrie																0	0
																0	0

Total number of interactions:  
 Interactions in focal samples only:

TABLE 7: Dominance matrix for High Tail group with three adult males.

	High Tail	Crest	Cowlick	Jane	Este	Slinky	Crook	Big	Corrie	Toto	Handle	Brush	Plum	Grub	I of Corrie	Sum
Ad ♂ High Tail	*	33	26	2	5	9	0	3	3	1	1	3	4	0	0	90
		10	8	1	1	3	0	0	0	0	0	1	3	0	0	27
Ad ♂ Crest		*	24	12	12	7	3	8	14	4	3	15	10	4	0	116
			11	5	3	0	1	2	9	1	1	6	4	1	0	44
Ad ♂ Cowlick			*	1	2	3	0	1	2	2	1	1	3	1	0	17
				0	1	1	0	1	0	1	1	1	1	1	0	8
Ad ♀ Jane				*	5	11	0	11	12	3	11	10	11	0	3	77
					3	7	0	5	9	0	6	6	3	0	1	40
Ad ♀ Este					*	11	0	15	18	0	3	10	10	0	1	68
						4	0	8	12	0	1	3	7	1	0	36
J2 ♀ Slinky						*	0	5	12	2	10	14	13	4	2	62
							0	2	3	1	2	5	7	2	1	23
Ad ♀ Crook							*	0	0	0	0	2	0	0	1	3
								0	0	0	0	0	0	0	0	0
Ad ♀ Big								*	12	0	2	9	10	1	0	34
									3	0	0	5	8	0	0	16
Ad ♀ Corrie									*	1	0	3	7	0	2	13
										0	0	1	3	0	0	4
J1 ♂ Toto										*	7	2	3	3	3	18
											0	0	2	0	0	2
J1 ♀ Handle											*	16	10	0	3	31
												4	1	0	0	5
J2 ♀ Brush												*	24	0	1	25
													15	0	0	15
J2 ♀ Plum													*	1	0	1
														0	0	0
I2 ♀ Grub														*	1	2
															0	0
I1 ♀ I of Corrie															*	0

Total number of interactions:  
Interactions in focal samples only:

557  
220

with adult males (cf. Rhine, 1973). Since these one-male groups showed the same patterns of dominance relationship reported for the large multi-male group, Alto's group, by Hausfater (1975), it is clear that the small size and high sex ratio in those groups had little effect on at least one aspect of social organization - dominance relations.

### Rates of Social Interaction

#### Rate Calculations

Rates of social interaction were calculated by dividing the number of interactions in which an individual or class of individuals participated, by the number of focal sample minutes of observation on that particular individual or class.

Appendices 1 and 2 summarize the rates of social interaction per hour between each pair of individuals for four categories of behavior: agonistic bouts, mounting, sexual presentation, and grooming. These rates were obtained by dividing the number of interactions between two individuals by their combined number of focal sample minutes, thus:

$$E = \frac{n_{iji} + n_{ijj}}{t_i + t_j} \quad (1)$$

Here  $n_{iji}$  equals the number of events done by  $i$  to  $j$  in individual  $i$ 's focal samples, plus  $n_{ijj}$ , the number of events done by  $i$  to  $j$  in  $j$ 's focal samples. The sum of these interactions is divided by the sum of focal sample minutes on individual  $i$  ( $t_i$ ) plus focal sample minutes on individual  $j$  ( $t_j$ ). The number of behaviors done by  $i$  to  $j$  may be recovered by multiplying the values in Appendices 1 and 2 by the number of focal sample minutes in each dyad given in Appendices 3 and 4.

The mean dyadic rates of interaction for each individual in each one-male group were calculated by:

$$\text{Rate of } i\text{'s interaction with all other group members, } j = \frac{\text{Interactions between } i \text{ and all other individuals, } j}{\text{Sum of } i\text{'s and } j\text{'s focal sample minutes}}$$

Or in mathematical terms:

$$\bar{L}_i = \frac{\xi_j (n_{ij} + n_{ji})}{\xi_j t_{ij}} \quad (2)$$

For example, assume that individual  $i$  is an adult female,  $\xi_j$  indicates that all events ( $n$ ) are summed in which individual  $i$  was a participant with all other individuals,  $j$ . Let  $n_{ij}$  equal the number of events done by  $i$  to all other individuals,  $j$ , and let  $n_{ji}$  equal the number of events done by all individuals  $j$  to the  $i^{\text{th}}$  female. Further, let  $\xi_j t_{ij}$  equal the number of minutes when both  $i$  and all other individuals,  $j$ , were present in the group.

This gives a mean rate of social interaction of individual  $i$  with all other group members (Tables 8 and 9).

Once these individual rates of interaction were obtained, a pooled, weighted mean rate of interaction for each age-sex class was calculated:

$$\bar{L}_h = \frac{\sum_i (\bar{L}_i \cdot k \cdot D_k)}{T} \quad (3)$$

Specifically, let  $\bar{L}_h$  equal the pooled mean rate of interaction of age-sex class  $h$  with all other individuals. Here  $\sum_i$  equals the sum of the individual mean rates for all individuals  $i$  in the  $h$  class. Because group composition did not remain constant and all group members consequently were not available for interaction for the same number of days, the  $k$  and  $D_k$  weighting terms were added. Let  $\bar{L}_i$  equal the mean dyadic rate of interaction when  $k$  dyads existed per adult female, for example. Let  $k$  equal the number of dyads and let  $D_k$  equal the number of days when  $k$  dyads existed in the group. Finally, let  $T$  equal the total number of days of observation. This calculation gives the rate of social interaction of an age-sex class with all other individuals, adjusted for changes in group composition (Tables 10 and 11).

### Social Interaction in One-Male Groups

Appendix 1 presents the rates of social interaction for all pairs of individuals in High Tail's group for any length of time while the group had only one adult male. Comparable data for BTF group are presented in Appendix 2. Cells with an asterisk are a priori zero since an individual could not aggress against, present to, or mount itself. The "mean rate" values give the mean rate of interaction for that individual with all other group members. Row mean rates indicate that the individual initiated the behaviors or won in an agonistic interaction; column mean rates indicate the rate at which that individual was the recipient of the behavior.

In High Tail's group adult female Este initiated agonistic interactions more frequently than any other group member while J2 female Brush received agonistic behaviors most often (Table 8). Adult female Crook groomed others most frequently and infants were groomed at the highest rate. Only male High Tail engaged in mounting. Although J2 female Brush presented more frequently than any other group member, she was never mounted, suggesting that these presentations were non-sexual behaviors. As would be expected, male High Tail was presented to most frequently. In BTF group as in High Tail group, the second ranking adult female, Nice in this case, initiated agonistic interactions most

TABLE 8: A summary of rates of social interaction per hour between dyads of individuals in High Tail group with only one adult male. Cell entries are read clockwise from upper left: agonism, groom, present, and mount.

	Initiator =	Row		Receiver =	Column	
		Mean	Rates		Mean	Rates
Ad ♂	High Tail	.173	.048	.000	.042	
		.017	.000	.000	.045	
Ad ♀	Jane	.164	.108	.025	.102	
		.000	.013	.013	.019	
Ad ♀	Este	.314	.090	.050	.150	
		.000	.006	.006	.031	
Ad ♀	Crook	.129	.263	.233	.134	
		.000	.037	.000	.043	
Ad ♀	Big	.075	.102	.086	.071	
		.000	.027	.000	.038	
Ad ♀	Corrie	.017	.097	.227	.102	
		.000	.017	.000	.011	
J2 ♀	Slinky	.204	.115	.058	.043	
		.000	.014	.000	.000	
J2 ♀	Brush	.044	.144	.379	.000	
		.000	.160	.000	.014	
J2 ♀	Plum	.000	.073	.237	.044	
		.000	.030	.000	.000	
J1 ♀	Handle	.000	.144	.054	.144	
		.000	.036	.000	.000	
J1 ♂	Toto	.000	.018	.090	.018	
		.000	.018	.000	.018	
I2 ♂	Grub	.000	.018	.036	.161	
		.000	.000	.000	.000	
I1 ♂	I of Big	.000	.000	.000	.215	
		.000	.000	.000	.000	
I1 ♂	I of Crook	.000	.000	.000	.179	
		.000	.000	.000	.000	
I1 ♀	I of Corrie	.000	.000	.000	.108	
		.000	.000	.000	.000	
Total Mean Rate of Interaction:			.108	.101		
			.002	.022		



TABLE 9: A summary of rates of social interaction per hour between dyads of individuals in BTF group. Cell entries are read clockwise from upper left: agonism, groom, present, and mount.

Initiator	Receiver	Row		Column	
		Mean	Rates	Mean	Rates
Ad ♂ Ki		.166	.054	.000	.048
		.014	.000	.000	.034
Ad ♀ Kala		.170	.045	.064	.054
		.000	.054	.003	.020
Ad ♀ Nice		.330	.144	.014	.114
		.000	.007	.003	.021
Ad ♀ BTF		.007	.099	.267	.115
		.000	.003	.007	.034
Ad ♀ Bent		.096	.097	.206	.107
		.000	.045	.007	.034
J2 ♀ Muffet		.078	.119	.174	.068
		.000	.034	.010	.000
J2 ♂ Joc		.270	.028	.048	.041
		.024	.005	.000	.029
J2 ♀ Teeka		.000	.076	.000	.000
		.038	.000	.000	.000
J1 ♀ Girl		.000	.090	.270	.056
		.000	.022	.009	.004
J1 ♂ Romulus		.000	.000	.056	.016
		.000	.000	.000	.000
J1 ♂ Remus		.000	.016	.095	.032
		.008	.008	.000	.000
I1 ♂ I of BTF		.000	.000	.008	.095
		.000	.000	.000	.000
I1 ♀ I of Nice		.000	.000	.000	.160
		.000	.000	.000	.000
Total Mean Rate of Interaction:		.126	.081	.004	.020

frequently (Table 9). Low ranking adult female BTF and J1 female Girl received the most agonism. Female Nice most frequently initiated grooming and her new-born infant, who was deformed at birth, was groomed more often than any other member. As no females were in estrous during the study period, no females in BTF group were mounted very often and two J2's, 1 male and 1 female, mounted others infrequently but at a higher rate than did male Ki. Adult female Kala presented most frequently; male Ki, females BTF and Bent were presented to with equal frequency.

Examining the behavior of the single adult males in each group, this study shows that High Tail directed most of his agonistic behaviors toward adult female Crook and toward the only other male, J1 male Toto. Most of High Tail's nonagonistic behaviors were directed toward adult female Jane, the only female who continued to cycle throughout the study period. High Tail likewise received the most nonagonistic behaviors from female Jane but was presented to most frequently by sexually immature J1 female Handle. In BTF group, adult male Ki directed most of his agonistic behaviors toward J1 female Girl. Most of Ki's nonagonistic behaviors were directed toward grooming an anestrous adult female, Kala, though he groomed himself with equal frequency. As mentioned above, there were no sexually receptive females in BTF group. Ki received the most nonagonistic behaviors from

adult female Nice. As the top ranking individuals in each group, neither High Tail nor Ki received agonistic behaviors from any other group member. In general, rates of social interaction were slightly, though not significantly, higher for all classes of individuals in High Tail group than in BTF group, probably due to the slightly larger group size of High Tail group (Table 10).

#### Comparison of One-Male Groups with Multi-Male Groups

Focal samples of adult and subadult male behavior were taken in Alto's group from 1 March 1972 through 3 September 1973, while focal samples of estrous females were taken for 14 months continuously (Hausfater, 1975). Alto's group was 2.3 times larger than High Tail group or BTF group and, as might be expected, the rates of interaction in Alto's group were very close to 2.3 times higher than in the two one-male groups studied. The rate of total interactions for adult males in Alto's group was 9.70 interactions per hour of which 6.48 per hour were agonistic and 3.22 per hour were nonagonistic (Table 10). In contrast, males High Tail and Ki averaged 3.52 interactions per hour, of which 2.08 per hour were agonistic and 1.44 per hour were nonagonistic. Another way to look at these data is that an adult male in a one-male group would participate in an agonistic bout on average once every 29 minutes while a male in a multi-

TABLE 10: The mean dyadic rates of social interaction per hour for two one-male groups and a multi-male group.

	<u>Grooming</u>	<u>Mounting</u>	<u>Presents</u>	<u>Total Non-agonistic</u>	<u>Agonistic</u>	<u>Total Interaction</u>
BTF Group						
Adult male	0.50	0.14	0.36	1.00	1.74	2.74
Ad females	1.32	0.06	0.35	1.73	2.02	3.75
Juv-2	1.19	0.14	0.26	1.59	2.46	4.05
J-1/Inf	0.93	0.05	0.11	1.09	1.30	2.39
All age-sex classes	0.98	0.10	0.27	1.35	1.88	3.23
High Tail 1-male Group						
Adult male	1.02	0.24	0.63	1.88	2.42	4.30
Ad females	2.03	0.04	0.45	2.53	2.41	4.94
Juv-2	1.02	0.00	0.95	1.98	3.56	5.54
J-1/Inf	2.01	0.00	0.00	2.01	0.42	2.43
All age-sex classes	1.52	0.07	0.51	2.10	2.13	4.23
Alto Group (multi-male)						
Adult males				3.22	6.48	9.70
Ad females (at D + 3)				3.62	3.26	6.85

male group would aggress or be aggressed against on average once every nine minutes of observation. It should be emphasized that the definition of "agonistic bouts" as used here includes interactions typically described as spatial displacements or surplantations to intense bouts of overt aggression or fights. Similarly, a male in the multi-male group interacted with some other individual only once every 17 minutes on average. Thus a characteristic of one-male groups, probably due to their small size, was a markedly decreased rate of social interaction: the pace of life was slower.

For most of the study period, adult females in the one-male groups were not cycling but were lactating or pregnant. Therefore data for the day of least sexual activity, that is, three days after perenial deturgence (cycle day  $D + 3$ , in the usual shorthand notation), were used to compare rates of social interaction for adult females in Alto's group with the rates for adult females in the one-male groups. The rate of total interactions for cycling adult females on  $D + 3$  in Alto's group was 6.85 interactions per hour, of which 3.26 per hour were agonistic and 3.62 interactions per hour were nonagonistic. In the one-male groups, adult females averaged 4.35 interactions per hour of which 2.22 per hour were agonistic and 2.13 per hour were nonagonistic. Consequently, an adult female in a one-male group would participate in an

agonistic bout on average once every 27 minutes while a female in a multi-male group would be involved in an agonistic interaction once every 18 minutes on average. An adult female in the multi-male group participated in some social behavior with another group member on average once every nine minutes while a female in one of the one-male groups interacted with some other individual only once every 14 minutes on average. It is possible that the lack of sexual activity alone may account for the lower than expected rate of adult female social interaction in the one-male groups when compared to females in the multi-male group.

#### Comparison of Sexual Behavior and Consortship in One-Male Groups with Multi-Male Groups

High Tail frequently mounted adult female Jane; adult female Este was also mounted but at a much lower rate. For High Tail, every mounting was a copulation, that is, he gave pelvic thrusts and fresh ejaculate was observed after every dismount. High Tail's matings with Jane were restricted to two to four days before perenial deturgesence (cycle days D - 4 through D - 2). These are the cycle days that laboratory studies have shown to be the optimal time for mating (Hendricks and Kraemer, 1971). The first ranking males in the multi-male group also restricted their copulations primarily

to these same cycle days, though lower ranking males showed little cycle day selectivity in their matings. High Tail also copulated with female Este during the cycle on which she became pregnant, though because the onset of her estrus was not observed, I cannot be certain of the precise timing of these matings within her cycle. All other adult females in High Tail's group were pregnant or lactating during the study period.

Unlike males in the multi-male study group, High Tail did not enter a true consort relationship with the receptive female; he rarely followed her closely and, of course, there were no other males from whom he could herd her away. Most often High Tail would only stay close to the female for one to two hours each morning and afternoon during the few cycle days when mating occurred.

#### Changes in Rates of Social Interaction as the Number of Adult Males Increased

From the above analyses, I expected the addition of a second and then a third adult male to High Tail group to result in successive increases in rates of social interaction for High Tail himself and for all other group members. In fact the results were contrary to my expectations: each additional adult male entering a previously one-male group resulted in a decreased rate of social interaction for High Tail and for all other

classes of individuals, as well.

High Tail's was a one-male group for 22 days of the study, a two-male group for 22.5 days, and a three-male group for 33.5 days during the study. Figure 1 presents the changes in rates of social interaction with the addition of two adult males; Tables 10 and 11 summarize mean rates of social interaction for every age-sex class when various numbers of males were present in High Tail's group. When the second male, Crest, joined High Tail group, there was no significant difference in the pooled rates of all classes for all social interactions, but the rate of interaction for most classes declined slightly. The rate of total social interaction declined further still when a third adult male, Cowlick, joined High Tail group. With the addition of these two males, High Tail's rate of interaction increased significantly (variance ratio,  $F_{\max} = 1.43$ ,  $df = 62, 130$ , .05 level). Whereas in the two-male group, High Tail participated in some social interaction on average once every 20 minutes and in a nonagonistic behavior only once every 41 minutes, in the three-male group, High Tail interacted with another group member once every 13 minutes on average and participated in a nonagonistic interaction once every 23 minutes. Crest's rate of interaction did not change when the third male joined but, like second-ranking males in the multi-male group, remained higher than



RATE OF SOCIAL INTERACTION OF  
HI TAIL GROUP  
WITH 1, 2, & 3 ADULT MALES

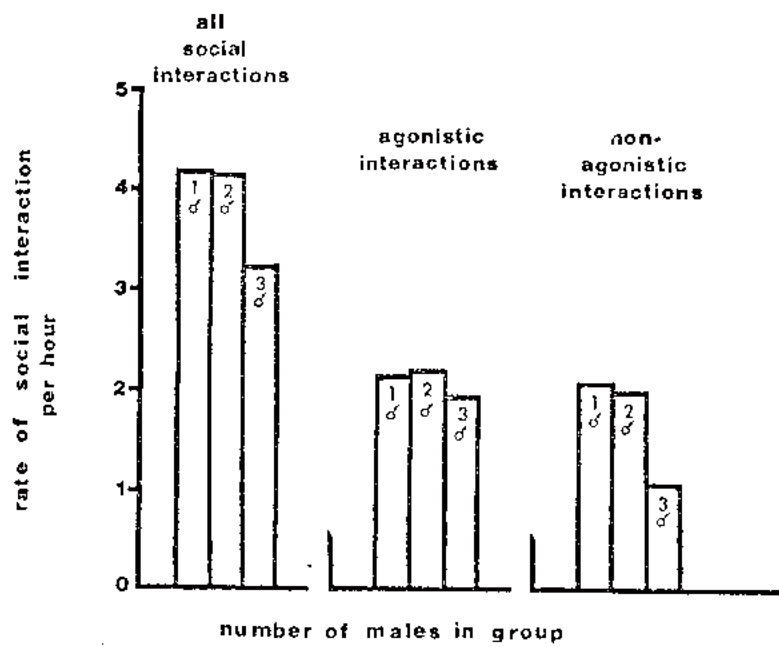


TABLE 11: The mean dyadic rates of social interaction per hour for High Tail group with two and three adult males.

	<u>Grooming</u>	<u>Mounting</u>	<u>Presents</u>	<u>Total Non-agonistic</u>	<u>Agonistic</u>	<u>Total Interaction</u>
High Tail 2-male Group						
Adult males	0.72	0.36	0.82	1.90	2.00	3.91
Ad females	1.70	0.18	0.35	2.23	1.50	3.73
Juv-2	1.07	0.04	0.55	1.66	2.86	4.51
J-1/Inf	2.13	0.00	0.10	2.23	0.66	2.89
All age-sex classes	1.41	0.15	0.46	2.02	2.18	4.21
High Tail 3-male Group						
Adult males	0.41	0.30	1.06	1.78	1.81	3.59
Ad females	0.57	0.11	0.60	1.28	2.05	3.33
Juv-2	0.35	0.03	0.59	0.97	2.61	3.58
J-1/Inf	0.64	0.00	0.12	0.76	1.04	1.80
All age-sex classes	0.49	0.11	0.60	1.20	1.97	3.21

High Tail's rate of interaction. Crest interacted with another individual on average once every 11 minutes. Before the third male joined the group, no male-male mountings had been observed; afterwards, Crest mounted High Tail and Cowlick mounted Crest on several occasions. In each case the mounter directed submissive gestures toward the mounted male.

The addition of two new males also resulted in a significant decrease in the total rate of interaction for adult females (variance ratio,  $F_{\max} = 1.48$ ,  $df = 406, 428$ , .01 level). A slight increase in the rate of agonistic interaction and a greater decrease in the rate of nonagonistic interaction resulted in a change from one interaction every 16 minutes for adult females in a one-male group to one interaction every 18 minutes for females in a three-male group. The total rate of interaction in both the J2 and J1/Inf classes also decreased significantly (variance ratio,  $F_{\max} = 1.31$ ,  $df = 306, 262$ , .05 level and variance ratio,  $F_{\max} = 1.67$ ,  $df = 96, 114$ , .01 level, respectively), reflecting a significant decrease in the rate of nonagonistic interaction (variance ratio,  $F_{\max} = 1.80$ ,  $df = 82, 96$ , .01 level for the J1 class and  $F_{\max} = 3.10$ ,  $df = 40, 88$ , .01 level for the J1/Inf class).

The addition of two adult males obviously affected the behavior of all age-sex classes in High Tail group.

The resulting changes cannot be accounted for by increasing group size, i.e. increased number of social partners, since an increase not a decrease in the rate of social interaction would have been predicted to accompany increased group size. It seems likely that the observed decrease in the rate of total social interaction resulted from greater inter-individual distances when first one and then another adult male joined High Tail group, though no quantitative data on spatial relationships are available. A similar change in the rate of social interaction among adult males occurred in the multi-male group as the number of estrous females increased, also probably due to increased inter-adult male distances (Hausfater, in press). Thus, it is likely an increase in inter-adult male distances resulted in decreased group density and probably was responsible for the lower rate of social interaction when additional adult males entered a previously one or two male group.

#### Progression Order

For the purposes of this analysis, a progression was defined as any more or less linearly ordered movement of the group on the ground. The single constraint under this definition was that the group's dispersion in the direction of movement had to be greater than its dispersion perpendicular to the line of movement. In practice

during a progression the group was dispersed elliptically with the long axis of the ellipse defining the direction of movement of the group. This elliptical arrangement was transcribed as a linear one-dimensional array of individuals by calling off the order in which each individual crossed a fixed "counting point", a shrub or log along the line of march. Only progressions in which all group members crossed the counting point and in which the order of all such individuals were recorded were analyzed. Furthermore, progressions were defined as "forced" if the group was running from or being chased by another group, a predator, or Masai tribesman. The progression was defined as "spontaneous" if the group began moving without conspicuous outside provocation.

The first analysis was merely an examination of the progression data for any highly consistent or rigid arrangement of individuals: for example, was the male always first in progression, last, or in the middle? As might be expected, no such consistent ordering was found. The progression data were then further analyzed to determine if some more subtly expressed regularities were present. Specifically, an attempt was made to determine if the single adult male (1) favored the front, back, or middle third of the progressions and (2) if the male's position differed in forced and spontaneous progressions. If the group did not divide evenly into

thirds, a single extra individual was placed in the center third; if two extra individuals were present, one was assigned to the first third and one to the last third of the progression order. An infant carried by an adult female was recorded as following that female.

In spontaneous progressions of one-male groups, the adult male was in the first third significantly more frequently than was expected under the null hypothesis of random placement of the male among thirds of the group. Of 137 spontaneous progressions of one-male groups, the single adult male was in the first third 89 times, in the center 9 times, and in the last third 39 times. This tendency for the adult male to favor the front of progressions was statistically significant ( $\text{Chi}^2$  one-sample test,  $X^2 = 71.48$ ,  $df = 2$ , .01 level). In a much smaller sample of 39 forced progressions, the adult male was in the first third 14 times, middle third 9 times, and last third 16 times. No statistically significant deviation from random placement of the adult male was found ( $\text{Chi}^2$  one-sample test,  $X^2 = 2.0$ ,  $df = 2$ , .05 level). Thus, in comparison to spontaneous progressions, there is an indication that the adult male shifted toward a more central or back position during forced movements of the group.

This difference in position of the adult male in progression indicates that during spontaneous group

movements, he is among the first to enter various areas of the group's home range, while during forced progressions, the male is closer to the pursuing danger by being in the back part of the group. Perhaps in this way his position is best suited to alert the group or to defend it from predators.

#### Predator Defense

Previous investigators ( DeVore and Hall, 1965; Stoltz and Saayman, 1970; Rowell, 1966; Altmann, 1970) have reported that adult male baboons defend their group against leopards or lions and, in fact, appear to chase the predator away from the group. Adult males engage in this behavior cooperatively rather than singly. Surely the chances of a lone adult male being successful in predator defense are near zero. Therefore, a behavior that might be appropriate for an adult male in a multi-male group could have disastrous consequences for the single adult male in a one-male baboon group.

On three occasions, the response to predators of an adult male in a one-male group was witnessed. Protocols of these three incidences taken from my field notes are given below:

High Tail group, 22 Feb. 1972, 1337: Loud alarm barks were given toward the vegetation south of Magi-Moto water hole. Herds of gazelle, ostrich, and zebra ran as two cheetah chased them west. High Tail, Jane, and

unidentified others in High Tail's group ran toward the cheetahs. The cheetahs stopped chasing and ran back toward the vegetation south of Magi-Moto. During the running, High Tail caught a juvenile gazelle (a yearling with six inch horns) and held it to the ground while trying to bite into its hind leg. When adult female Este approached, High Tail looked up and the gazelle escaped, running back to the herd.

The fact that females and juveniles joined High Tail in defense of the group from predators demonstrated that cooperative defense behavior against predators was not a pattern of behavior unique to adult male baboons. The capture of the gazelle by High Tail at this time of presumed conflict over avoidance of or approach toward the predator fits the classical model of a "displacement behavior".

On another occasion, two hyenas approached to within 150 feet of High Tail group and stared toward the baboons. High Tail group grew compact and watchful but did not run. The portion of the group that was closer to the predators, moved quickly toward the other half. Male High Tail was at the rear of this progression and therefore closest to the hyenas. He did not run toward them and the group did not give alarm barks.

In the last case of predator defense, a Masai dog elicited an alarm response from BTF group:

BTF group, 5 June 1972. 1440: Two Masai men were seen in the distance. The adult male of BTF group, Ki, descended a



tree, approached the rest of his group, and looked at each one until all ran north. No alarm barks were given. Ki climbed another tree and stared toward the Masaii; he repeated this behavior several times.

1449 Ki sat in a tree and gave two single-phase alarm barks toward the two Masaii men and their dog as they sat 400 feet away.

1457 Ki ran 100 feet toward the Masaii and dog while other members of BTF group sat compact, stared at Ki, and gave cohesion grunts.

1458 The Masaii walked on; Ki ran toward the dog and the dog ran away.

1505 BTF group gave cohesion grunts as Ki walked part way back to the group; the group then resumed feeding.

In sum, even a lone adult male continued to run toward a predator, but other non-male group members sometimes aided in the predator defense. When a predator was spotted at a distance, most group members including the adult male, stayed at a safe distance from the predator; thus an approach or chase of a predator by several individuals might be necessary only when the predator was close enough actually to harm one of the group members.

#### Comparison of Hamadryas and Yellow Baboon One-Male Groups

As mentioned earlier, the genus Papio apparently included two types of group organization. The savannah baboons (Papio cynocephalus, P. anubis, and P. ursinus) typically live in multi-male, multi-female groups while hamadryas baboons (P. hamadryas) live in one-male units or harems by day and aggregate into multi-male "bands"

and larger "troops" only on sleeping cliffs at night (Kummer, 1968). With this study of one-male groups of savannah baboons, one is able now to ask how this form of social organization compared between two species of baboons.

At a gross level, the role of the single adult male in P. hamadryas one-male units was similar to the role of the adult male in P. cynocephalus one-male groups. In both species, the adult male mates with sexually receptive females in his group and aids in defense from predators. The two species differ in that savannah one-male groups do not aggregate into larger units at night but sleep as a group in a grove of yellow barked acacia trees; thus P. cynocephalus one-male groups are in some ways more autonomous or independent than are P. hamadryas units. A second difference in the two species is evident in herding behavior. Hamadryas males maintain their harems by threatening or biting their females on the neck; the females respond by running toward the male and thereby remaining close to the unit leader. By contrast, in the consort relationship between an adult male yellow baboon and an estrous female, the male herds her away from other males by nipping at the flank of the female, to which she responds by moving forward. The difference lies in the direction of the female's response.

Hausfater (1975) has suggested that the one-male

hamadryas units are a specialization evolving from the behavioral components of herding behavior in yellow baboons coupled with the counter-chase response in which an individual giving submissive gestures runs toward the aggressor. This concept of an evolved social organization points out the last, more basic difference between one-male groups in both species: P. hamadryas has evolved in its desert habitat over many generations while the one-male groups of yellow baboons in Amboseli are a recent, possibly ephemeral result of a declining baboon population and probably represent the "tails" of this shifting population distribution. In sum, one-male units of hamadryas baboons are uniquely adapted to their xerophytic habitat; one-male groups of yellow baboons are not.

#### IV. SUMMARY AND CONCLUSIONS

This study has shown that contrary to the prediction of Crook and Gartlan's (1966) socioecology model, one-male groups of yellow baboons, at least in Amboseli, are not an adaptive response to an increasingly xerophytic habitat. The study, however, does support an implicit and usually unstated assumption of socioecology models, which is that groups at the ends of the range of variability in size and composition would suffer compared to groups nearer the modal size and composition for that habitat. I have shown that the extent of role specialization in savannah baboon groups is not nearly as great as has been implied ( DeVore and Hall, 1965): females as well as males defend the group against predators and the single adult male maintains no absolutely fixed position in group progressions, though clear tendencies in his placement were evident. This study showed that dominance relationships remained stable regardless of the estrous states of the females or of the number of males in the group. Finally, it showed that the rate of social interaction was not only a function of group size since additional adult males did not cause an increase in rate of interactions, but also reflected changes in the number and probably spacing of adult males in the group. Thus, rates of social interaction were shown to be dependent

not merely on the number of social partners available,  
but on the specific age and sex of these partners.

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