2002

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Larissa Swedell
CUNY Queens College

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Previous researchers of hamadryas baboons have described a star-shaped sociogram, whereby the strongest social bonds within hamadryas one-male units are between a leader male and his females and bonds among females are weak by comparison. This type of social organization is also known as cross-bonding to distinguish it from the female-bonding found in most papionin monkeys. Models of female primate socioecology suggest that hamadryas baboons lack female bonding due to their reliance on scarce, widely-dispersed food resources. Here, I report observational data from a wild population of hamadryas baboons in Ethiopia indicating that, while females varied widely in their frequency of social interaction with other females, most females spent about as much social time with other females as they did with the leader male and some females even crossed unit boundaries to interact with one another. The size of a unit was positively correlated with the tendency of its females to interact with other females and was negatively correlated with the tendency of its females to interact with the leader male. Females were equally likely to spend social time with other females whether or not the leader male was available for social interaction at the time. Overall, this study suggests that a star-shaped sociogram does not characterize all hamadryas baboons and that female hamadryas may be, to some extent, female-bonded as well as cross-bonded. The lack of more pronounced female bonding in hamadryas is probably due to the behavior of males rather than to ecological factors.

KEY WORDS: hamadryas baboons; female bonding; cross-bonding; star-shaped sociogram; female social relationships; grooming.

[1]Department of Anthropology, Queens College, City University of New York, Flushing, New York; e-mail: lswedell@qc.edu.

INTRODUCTION

Kummer (1968) and Abegglen (1984) characterized the social system of hamadryas baboons (*Papio hamadryas hamadryas*) as having multiple levels of organization in which the smallest and most stable social unit is the one-male unit (OMU), consisting of a leader male, ≥ 1 females, their offspring, and sometimes ≥ 1 follower males. The cohesiveness of one-male units is maintained via aggressive herding by leader males, and hamadryas social structure as a whole is maintained by the behavior of and relationships among males, who compete and cooperate with one another over access to and control of females (Abegglen, 1984; Kummer, 1968).

Previous research, both in the wild and in captivity, has described hamadryas one-male units as having a star-shaped sociogram, wherein each female has a far stronger bond with her leader male than with any other adult member of her unit. These bonds are expressed in the tendency of hamadryas females to groom and to interact predominantly with the leader male and rarely with other females (Abegglen, 1984; Kummer, 1968; Sigg, 1980). Kummer (1968) described social activity within hamadryas OMU's as occurring along two main avenues: between the leader male and each of his females and between females and their offspring. He noted that "this star-shaped pattern, the center of which is the male, keeps the unit together. In most of the units, other possible interactions, as those . . . between females and females, are not more frequent than contacts with strangers" (Kummer, 1968, pp. 80–81). In this model, there are only two major social strata of adult group members, a dominant individual—the leader male—and several relatively undifferentiated subordinates—the females—and most interactions occur between the dominant individual and each subordinate rather than among the subordinates. In captivity, when a group of hamadryas females is left alone to interact in the absence of a male, the same social organization often resurfaces in a different form: one female assumes the dominant role of the leader, all other females remain relatively undifferentiated, and most social interactions occur between the dominant female and each of the other females rather than among the other females (Coelho *et al.*, 1983; Pfeiffer *et al.*, 1985; Stammbach, 1978). Because the star-shaped pattern persists even when males are removed, researchers have concluded that this social organization is not imposed on females by males, but instead that hamadryas females have an innate tendency to form social units oriented around a single central individual (Coelho *et al.*, 1983; Stammbach, 1978).

Byrne *et al*. (1989) proposed the term cross-sex bonding to describe a hamadryas-like social organization in which intersexual affiliative bonds are stronger than intrasexual bonds. Byrne *et al*. distinguished cross-bonding from the female-bonded (Wrangham, 1980) organization that has been

reported for most populations of savanna baboons, particularly *Papio hamadryas anubis* and *P. h. cynocephalus* (Altmann, 1980; Barton *et al.*, 1996; Dunbar, 1983; Henzi *et al.*, 1997, 2000; Melnick and Pearl, 1987; Saunders, 1988; Seyfarth, 1976; Silk *et al.*, 1999). In particular, Byrne *et al.* (1989) suggested that mountain baboons (*Papio hamadryas ursinus*) might be more accurately characterized as cross-bonded rather than female-bonded, and that this distinction would obviously apply to hamadryas baboons as well.

Whether a baboon population will be cross-bonded or female-bonded might be explained by patterns of food distribution and predation, which have been argued to be primary determinants of the structure and patterning of social relationships among female primates (Barton *et al.*, 1996; Isbell, 1991; Sterck *et al.*, 1997; van Schaik, 1989; Wrangham, 1980). When food is clumped and defensible, promoting intra-group contest competition, females will remain in their natal groups and will form differentiated, kinship-based affiliative and agonistic relationships, *i.e.*, they will be female-bonded. When food is more evenly distributed and does not promote contest competition, females should not benefit from forming kin-based alliances and should therefore disperse from their natal groups and develop weak, if any, bonds with other females. Traditionally, savanna baboons, including anubis, yellow, and some populations of chacmas, have been placed in the former category, whereas hamadryas baboons have been placed in the latter (Barton *et al.*, 1996; Sterck *et al.*, 1997; Wrangham, 1980). Among chacma baboons (*Papio hamadryas ursinus*), the degree of female-bonding vs. cross-bonding may vary depending on a number of factors, including food distribution, predator pressure, altitude, and group size (Anderson, 1990; Byrne *et al.*, 1989; Hamilton and Bulger, 1992; Henzi *et al.*, 1997, 2000), and this may be the case for guinea baboons (*P. h. papio*) as well (Anderson and McGrew, 1984; Boese, 1975; Byrne, 1981; Dunbar and Nathan, 1972). Within the context of this model, the weak affiliative and agonistic relationships among females that have been reported for wild hamadryas (Abegglen, 1984; Kummer, 1968; Sigg, 1980) can be easily explained by the scarcity and wide dispersion of food resources that typify hamadryas habitats (Barton, 2000; Barton *et al.*, 1996; Wrangham, 1980).

Although relationships among hamadryas females in the wild have been reported to be relatively undeveloped and undifferentiated (Abegglen, 1984; Kummer, 1968), no study of wild hamadryas focused specifically on social interactions among females. Captive hamadryas females, which have been studied extensively, exhibit both dominance and grooming relationships, especially in the absence of males (Chalyan *et al.*, 1991; Coelho *et al.*, 1983; Colmenares *et al.*, 1994; Gore, 1991; Leinfelder *et al.*, 2001; Stammbach, 1978; Sigg, 1980; Stammbach and Kummer, 1982; Vervaecke *et al.*, 1992; Zaragoza *et al.*, 1996). Given that other aspects of hamadryas behavior, such

as the one-male unit social structure and male herding, are little modified by captivity (Kummer and Kurt, 1965), the same might be true of female behavior. If so, then the lack of evidence for differentiated relationships among females in wild hamadryas may be due to a lack of relevant data rather than to a lack of such relationships.

I used data from a two-year study of hamadryas baboons in Ethiopia to test the commonly-held assumption that hamadryas females are bonded only to their leader males and that relationships among females are weak or absent. Specifically, I examined the following two hypotheses: (1) Hamadryas one-male units can be characterized as a star-shaped sociogram. This hypothesis predicts that rates of social interaction between each female and her leader male are far greater than those among females. (2) The scarce, widely dispersed food resources in hamadryas habitats result in little or no feeding competition among females, leading to a non-female-bonded system. This hypothesis predicts that (a) females rarely interact competitively and cannot be ordered into a dominance hierarchy and (b) females rarely interact affiliatively and have weak and undifferentiated affiliative relationships.

METHODS

Study Site and Subjects

The study population inhabits a region surrounding the Filoha outpost of the Awash National Park, about 150 km east of Addis Ababa, Ethiopia, in the semi-arid lowlands of the northern Rift Valley of East Africa. The southern boundary of the park includes a zone of hybridization between hamadryas and anubis baboons that has been the subject of long-term study by the Awash National Park Baboon Research Project (Beyene, 1993; Nystrom, 1992; Phillips-Conroy *et al.*, 1991, 1992; Phillips-Conroy and Jolly, 1981, 1986). The Filoha outpost lies in the far north of the park, about 40 km north of the baboon hybrid zone. An area of about 5 km^2 immediately surrounding the Filoha outpost is covered by hot springs ('fil woha' means hot water in Amharic) and doum palm trees (*Hyphaene thebaica*), but the predominant vegetation in the surrounding area and throughout the northern part of the park is an *Acacia*-dominated thornscrub characteristic of hamadryas habitat in other parts of Ethiopia.

Although this population is relatively close to the hamadryas-anubis hybrid zone, it shows no obvious phenotypic signs of anubis admixture, as individuals are virtually indistinguishable from those observed by Kummer (1995, 1998) at Erer Gota, Ethiopia. At least 5 groups (aka bands Kummer, 1968) of hamadryas baboons range throughout the Filoha area and alternate

between numerous sleeping cliffs, 5–10 km apart. One of the cliffs is about 200 m from the Filoha outpost and a second is near the village of Wasaro, 5 km from Filoha. The study group numbered about 150 individuals in November 1996 and 170 individuals in September 1998. The number of females of reproductive age ranged from 45 to 55 and the number of OMU's (and leader males) ranged from 22 to 25.

Data Collection

I habituated the study group from late October 1996 through January 1997 and began data collection in February 1997. Data collection was interrupted by a field accident in May 1997, resumed in December 1997, and continued through September 1998, totaling 262 observation days and 985 contact hours between November 1996 and September 1998. I conducted behavioral observations every day when the study group had slept at the Filoha cliff the previous night, and, when possible, also on days when they had slept at the Wasaro cliff the previous night. Starting at dawn, I followed the group for as long as possible each day. When a known OMU came into view, I immediately conducted a scan sample of that unit, recording the activity of all of its members, each female's nearest adult or subadult neighbor, and each female's proximity to the leader male. I repeated scans at 10-min intervals for as long as that OMU was in view. If a second OMU came into view, I began scan samples at 10-min intervals for that unit, staggering the scans so that those for two OMU's did not occur at the same time. I also made observations *ad libitum* (Altmann, 1974) on mating and agonistic behavior among adult individuals and conducted 30-min continuous focal samples of estrous females. Because the focal samples are limited in number (due to visibility problems) and unevenly distributed across females, I did not use them in the quantitative analyses reported here.

I did not construct female dominance hierarchies because there were no consistently unidirectional interactions among females that would indicate dominance relationships. Females occasionally fought, but the fights appeared to be exclusively over grooming access to the leader male and were usually undecided, in that there was no discernable winner or loser, nor did one female display submissive gestures to the other (such as crouching, which female hamadryas perform when they receive aggression from males). Instead, the initial target of the aggression would either ignore it and continue grooming the leader male or return it with threats, while continuing to groom the male, and the aggression would eventually subside. I also did not collect systematic data on feeding behavior because preliminary observations suggested that females did not displace one another at food resources or fight in the context of feeding. I confirmed this impression with

subsequent observations. Although not determinable with certainty due to the type of data collected, females also did not appear to differ in the rate at which they were able to obtain food. Qualitative observations suggested that females and males avoided feeding competition by spreading out during foraging.

Data Analysis

Data from 39 females (see Table I), distributed across 17 one-male units, contributed to these analyses. The number of females per unit ranged from one to 5, averaging 2.6 females per unit. I subdivided data for 2 females, FAN and VEN, due to changes in the size and composition of their OMU's. I considered data on FAN from the first season, when she was the only female in her unit, separately from data from the second season, when her unit contained 4 females. Similarly, I subdivided data on VEN into those collected when there were 2 females in her unit and those collected when there were 3 females in her unit. FAN and VEN therefore each count as 2 females for the purposes of these analyses.

From the OMU scan sample data, I tabulated per-female totals for each activity. I eliminated the behavioral categories walk, run, travel (walking or running in coordination with the other members of the OMU), forage (using hands to manipulate parts of plants, turning over rocks, or digging in ground, followed by putting food items into the mouth), eat (chewing and swallowing), and drink from the analysis because (a) the baboons were typically less visible when engaged in these activities, and their relative frequency would therefore have been underestimated and (b) I considered them to be subsistence activities rather than social activities and, as such, they would not reflect social preferences or relationships. The elimination of these categories resulted in new totals for each female that represented times when they were not engaged in subsistence activities and were therefore available for social activity. I divided the number of scan samples spent resting (sitting alone) or engaged in each type of social activity—sitting close, grooming, or being groomed—by this new total, resulting in a per-female percentage of available social time (calculated as a percentage of scan samples) spent in each social activity.

I used only a portion of scan sample data for these analyses. Because this paper is focused on female social behavior rather than mating behavior, I included only scans during which females were anestrous, *i.e.*, not sexually swollen and not engaging in mating behavior. Sexually swollen females, compared to anestrous females, maintain closer proximity to, receive more grooming from, and are herded more by leader males (Swedell, 2000a)

Table I. Percentage of scan samples during which females sat close to or groomed with their leader male or another female

Name and number of scan samples per female		Sitting close		Grooming or being groomed		Sitting close to, grooming, or being groomed total	
Name	Number of scan samples	To leader male	To another female	By another male	By another female	With leader male	With another female
Females in 1-female units							
URS	83	14	0	32	0	46	0
JUL	66	14	0	36	0	50	0
FAN	34	27	0	27	0	54	0
VIR	30	40	0	36	0	76	0
JUA	31	27	0	40	0	67	0
Females in 2-female units							
ANT	72	11	9	7	6	18	15
LIN	72	8	8	22	4	30	12
VER	124	16	0	40	0	56	0
AUD	218	9	1	7	0	16	1
VEN1	118	15	3	4	4	19	7
SER	78	17	5	24	5	41	10
CLE	46	3	8	16	3	19	11
MAR	123	14	8	16	2	30	10
Females in 3-female units							
KAT	50	5	0	5	5	10	5
OPH	50	13	4	10	0	23	4
VEN2	39	6	9	0	23	6	32
Females in 4-female units							
BEL	108	9	13	13	11	22	24
RAQ	152	4	25	3	14	7	39
NET	86	2	21	5	26	7	47
FAN2	81	5	13	13	25	18	38
WHO	161	4	17	10	11	14	28
IRI	42	0	25	15	11	15	36
CLA	54	9	13	15	8	24	21
ZEN	42	15	18	11	11	26	29
VIO	42	15	11	7	4	22	15
ROS	42	8	10	21	0	29	10
JUD	63	3	33	13	36	16	69
PAT	78	2	22	6	9	8	31
SEL	56	6	0	16	12	22	12
MIR	54	6	15	12	27	18	42
TYN	55	0	19	0	23	0	42
Females in 5-female units							
ANJ	122	2	34	12	14	14	48
ELE	121	8	33	13	18	21	51
CHI	83	11	33	24	0	35	33
ROM	83	5	27	14	15	19	42
GIN	77	4	35	5	16	9	51
TON	117	1	18	0	19	1	37
SYL	88	3	27	16	25	19	52
ISA	83	3	32	3	19	6	51
Mean Values	80.1	9.3	14.1	14.6	10.4	23.9	24.5

and are therefore more constrained by male behavior and less likely to be self-motivated in their actions. Because females spend most of their time pregnant or lactating, *i.e.*, anestrous, and in order to control for the effects of sexual swellings on female social behavior, I did not consider scan data from times when females were sexually swollen.

Moreover, because the number of scan-samples per female varied widely, I conducted exploratory data analysis to determine how many scan samples were representative of each female. First, I compared results obtained when including various subsets of females in the analysis and found that mean percentages of scan samples spent in each type of social activity, averaged across all females, never varied by >2.8 percentage points whether I used data only from females for which I had ≥100 scans, ≥50 scans, ≥30 scans, or ≥20 scans. In most cases, results using ≥20 scans differed from those using ≥30 scans to a greater extent than those using ≥30 scans differed from those using ≥50 or ≥100 scans. It thus appeared that once a minimum of 30 scans was reached, general patterns of female social activity and proximity changed only minimally as more data were added.

I also divided datasets for each female randomly into two halves and compared them to evaluate consistency in patterns of results for each female. Each random half of data sets of ≥30 scans did not differ from the other in its broad patterns, whereas data sets of ≤30 scans could not be consistently divided randomly to produce qualitatively similar halves. Based on the results of these two analyses, I set the per-female minimum at 30 scans. As a result, 39 females are included in the analysis, and the number of scan samples per female ranges from 30 to 218, averaging 80 scans per female.

To investigate patterns of female social activity, I compared the percentage of scan samples in which each female engaged in the following activities: sitting alone, sitting close, grooming, and being groomed. I defined sitting alone as sitting ≥10 cm from any other individual and not interacting socially. I defined sitting close as sitting so that one's torso, arm, leg, or head, *i.e.*, any body part except the tail, is <10 cm of another adult or subadult individual. I chose a distance of 10 cm because it appeared to most consistently reflect social engagement between 2 individuals, whereas greater distances (such as 1 m) were common among individuals that were in the same unit but rarely interacted socially. I considered sitting close to be a form of affiliative behavior because it was often interspersed with grooming bouts and appeared to mainly characterize dyads that showed other evidence of a close social relationship, such as frequent grooming and lipsmacking. In other primate taxa close spatial proximity has been shown to be a valid measure of social relationships and also to function as reconciliatory behavior after a conflict (Cords, 1993, 1997).

All behavioral categories were mutually exclusive: a female either sat alone, sat close to her leader male, sat close to ≥1 female, sat close to her leader male and ≥1 female (one on either side of her), groomed her leader male, groomed a female, was being groomed by her leader male, or was being groomed by a female. I did not include scans during which a female sat close to both her leader male and another female because in these cases the female's primary social partner was unclear, and I therefore could not exclusively categorize these scans as time spent with the leader male versus another female. I also did not include the relatively few scans during which a female interacted with an individual other than her leader male or another female, *e.g.*, a follower or solitary male, because the primary purpose of the analysis was to compare rates of interaction among females to those between females and leader males. Unfortunately, the amount of scan data per female was insufficient to compare rates of grooming among female dyads or grooming reciprocity within dyads.

RESULTS

General Patterns of Social Activity

For all results, percentages of time refer to percentages of a female's available social time, calculated from the scan samples. On average, females spent about 39% of their time sitting alone and about 61% of their time interacting socially with another individual: either their leader male, another female, a follower male, a juvenile, or a member of another unit. Females spent, on average, 9% of their time sitting close to their leader male, 14% sitting close to another female, 11% grooming their leader male, 5% grooming another female, 4% being groomed by their leader male, and 5% being groomed by another female (N = 39; Fig. 1). For purposes of comparison with Kummer's (1968) findings, Figure 2 shows the distribution of grooming activity among the members of two OMU's: LEO's unit (5 females) and ALE's unit (4 females). Each of them remained stable in membership and relatively consistent in patterns of social interaction for the entire length of the second observation season.

Variation Among Females

The above averages conceal wide variation in female-female social interactions. Of the females whose units contained ≥1 other female, 5 (VER, AUD, OPH, ROS, and CHI) never groomed or were groomed by another female, whereas 5 (NET, FAN, JUD, MIR, and SYL) spent ≥25% of their social time engaged in such interactions. Of the 7 females that spent ≥20%
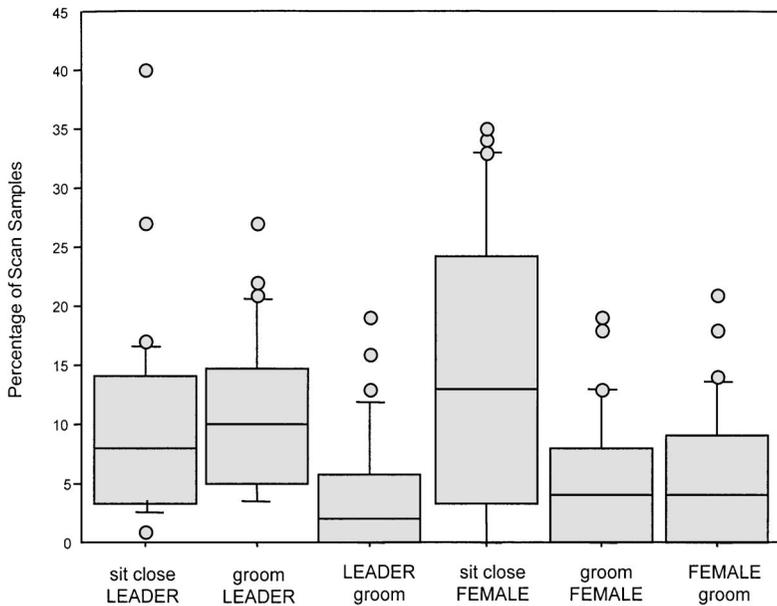
Fig. 1. Percentage of available social time (calculated from scan samples) spent by anestrous females sitting close to, grooming, or being groomed by their leader male or another female (boxes represent the standard error of the mean, vertical lines represent the standard deviation of the mean, and filled circles are points beyond the standard deviation; N = 39).

of their social time in grooming interactions with other females, 3 (NET, FAN2, & JUD) were members of ALE's unit (Fig. 2), in which by far the greatest number of interfemale interactions occurred. ALE's unit included 4 females, each of which spent ≥25% of her social time grooming with other females.

Of the remaining 4 females that spent ≥20% of their social time with other females, another two (MIR and TYN) were members of the same unit, and many of their grooming interactions were with each other. The remaining 2 females that spent ≥20% of their social time with other females were in two separate units, a 3-female unit (VEN2) and a 5-female unit (SYL), and they each split the time among the other females in their unit.

By contrast, 2 of the 5 females that never groomed or were groomed by other females (VER and AUD) were in the same 2-female OMU. These females rarely sat near one another and each was typically closer to the leader male than to one another. Also, one female (CHI) never groomed or was groomed by other females despite the fact that there were 4 other females in her unit and 3 of them (ROM, GIN, and ISA) spent ≥15% of their social time in grooming interactions with each other.
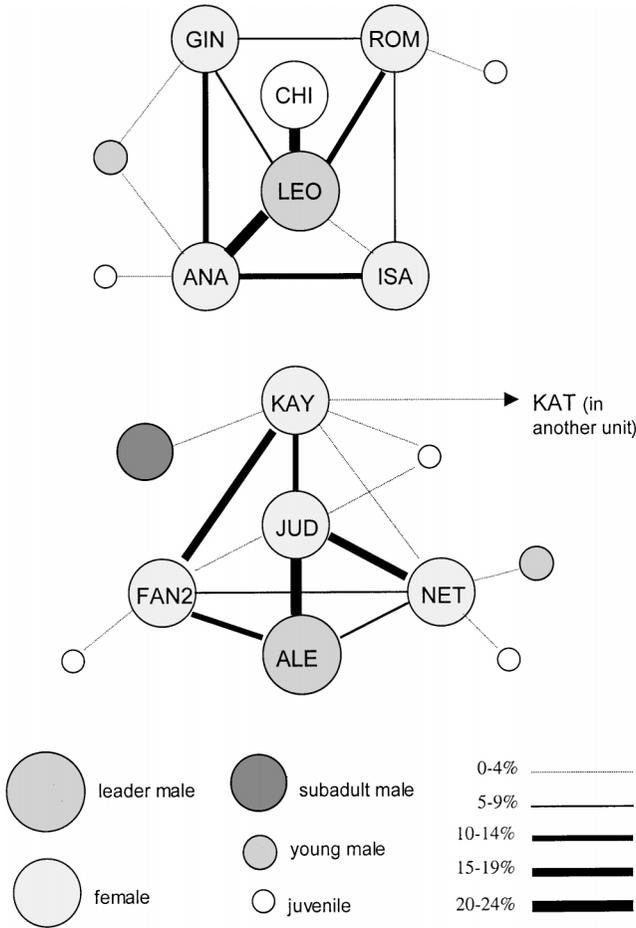
Fig. 2. Sociograms of LEO's and ALE's units, based on percentage of scan samples spent by each dyad in grooming interactions.

Effect of the Number of Females in a One-Male Unit

The number of females in an OMU was the most important factor affecting variation in rates of interaction among females (Fig. 3). Females in one-female units (N = 5) did not interact socially with other adult females. Females in 2-female units (N = 8) spent an average of 8% of their time in social contact with the other female in their unit and an average of 29% of their time in social contact with their leader male (averages are across all females in each unit-size category). Females in 3-female units (N = 3) spent an average
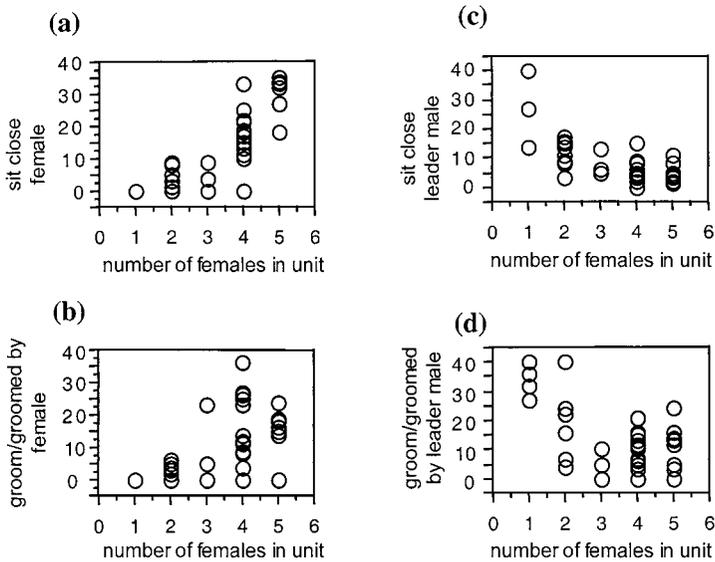
(a)

(c)

(b)

(d)

Fig. 3. Relationship between the number of females in a one-male unit and the percentage of available social time (calculated from scan samples) spent by anestrous females (a) sitting close to another female (Spearman Rank Correlation $r_s = .882$, $p < .0001$), (b) grooming or being groomed by another female ($r_s = .684$, $p < .0001$), (c) sitting close to their leader male ($r_s = -.575$, $p < .001$), and (d) grooming or being groomed by their leader male ($r_s = -.374$, $p = .021$).

of 13% of their time with the leader and 14% with other females; females in 4-female units (N = 15) spent an average of 17% of their time with the leader and 32% with other females; and females in 5-female units (N = 8) spent an average of 16% of their time with the leader and 46% with other females. The number of females in an OMU was positively correlated with the amount of time a female spent sitting close to (Spearman Rank Correlation $r_s = .882$, $p < .0001$, $n = 39$) or in grooming interactions with ($r_s = .684$, $p < .0001$, $n = 39$) another female in her OMU, and was negatively correlated with the amount of time a female in that OMU spent sitting close to ($r_s = -.575$, $p < .001$, $n = 39$) or in grooming interactions with ($r_s = -.374$, $p = .021$, $n = 39$) her leader male (Fig. 3 a-d). Because sit close and groom are mutually exclusive (*e.g.*, if a female sat close to and groomed a male, I recorded her as grooming him but not sitting close to him), the two sets of correlations provide independent measures of levels of social interaction among various dyads.

The effect of unit size on interactions among females is illustrated by a change in the frequency of such interactions by two females whose units

changed size during the study period. FAN, when in an OMU that consisted solely of herself and a leader male, did not interact with other females. However, when in an OMU with 3 other females, FAN spent 24% of her time in female-female grooming interactions. Similarly, when in an OMU with only one other female, VEN spent only 4% of her time grooming with her, but when in a unit with 2 other females, she spent 23% of her time grooming with other females.

Even within unit size categories females varied widely in the amount of time they spent with other females (Fig. 3). The 8 females in 2-female units ranged from 0 to 15%, the 3 females in 3-female units ranged from 4 to 32%, the 15 females in 4-female units ranged from 10 to 69%, and the 8 females in 5-female units ranged from 33 to 51%.

Interactions Between One-Male Units

On 13 occasions during focal sampling and observations *ad libitum*, I observed females from different one-male units interacting with one another. Most of these interactions were directed toward females with young infants. Three of them consisted of a female from one OMU approaching and sitting ≤10 cm from a female in another OMU for ≥20 sec. Another 3 of the interactions involved grooming, and 2 of those involved the same pair of females. The first time, the leader male of one of the females chased her and tried to neckbite her, but she escaped into a tree. The second time, the grooming bout lasted >20 min with no interference on the part of either leader male, though both watched the grooming session almost continuously. The third case of inter-unit grooming involved 2 other females, one of whose leader male was >30 m away at the time; the bout lasted 15 min.

Social Availability

Because female-female interactions appeared to increase with unit size, I examined the possibility that the identity of a female's social partner was a function of simple social availability. I compared the percentage of scan samples that each female spent in social contact with her leader male or another female with the percentages that would be expected based on the number of other unit members. The leader male of the OMU, adult and subadult females, and adult or subadult non-leader males that were consistent followers of the OMU were all included as unit members. I excluded other individuals that females interacted with rarely, such as solitary males, juveniles, and members of other OMU's, from the analysis. I also excluded females in one-female OMU's (N = 5), because these lacked the corresponding

observed vs. expected values for time spent with females, *i.e.*, both were equal to zero. For all units with ≥ 2 females (N = 34), I calculated expected percentages as a percentage of the total number of adult or subadult individuals in the OMU. For example, females in 2-female units, when not sitting alone, should spend 50% of their social time with the leader male and 50% with the other female in their unit; females in 3-female units should spend 33% of their social time with their leader male and 66% with other females (33% with each female); and females in OMU's with 2 females and one follower male should spend 25% of their social time with the leader male, 50% with other females (25% with each one), and 25% with the follower male. A comparison of observed with expected percentages revealed that about half (17) of the females spent more time than expected and half (16) spent less time than expected in social contact with the leader male (one female, ANJ, spent about as much time as expected with her leader male). By contrast, the vast majority of females (29) spent less time than expected in social contact with other females, whereas only 4 females spent more time than expected and one female spent about as much time as expected with other females. Females that spent less time than expected with both the leader male and other females spent the balance of their time interacting with juveniles, members of other units, and follower males. The distribution of grooming time among female dyads could not be determined with statistical accuracy due to insufficient scan data per female.

Social Availability of the Leader Male

To determine if females were interacting with other females only when the leader male was not available for social interaction, I examined the activity of the leader male during each scan sample in which 2 females in his unit were sitting close or grooming. I classified the leader male as being socially available when he sat alone, ≥ 10 cm from any other individual, and was not interacting socially with another individual. Because females in one-female units never interacted socially with other females and neither female in one 2-female unit (VER and AUD) interacted with the other, only 11 OMU's (and 32 females) contributed to the analysis. Of all samples in which 2 females sat close, the leader male was socially available on average 41% of the time, sat close to another individual on average 33% of the time, and groomed or was being groomed by another individual on average 26% of the time. Of all samples in which 2 females groomed one another, the leader male was socially available on average 52% of the time, sat close to another individual on average 18% of the time, and groomed or was being groomed by another individual on average 30% of the time. These results suggest that females did not limit their interactions with other females to times when the

leader male was unavailable for social interaction, but instead interacted with other females equally often regardless of whether the leader male was socially occupied at the time.

DISCUSSION

The levels of social interaction shown by Filoha females contrast with those from previous studies of wild hamadryas baboons. While most females at Erer-Gota (Kummer, 1968) and Awash Station (Nagel, 1971) interacted far more with leader males than with other females, most Filoha females interacted at least as much with other females as they did with leader males. The average numbers of females per one-male unit in Kummer's and Nagel's study groups, however, were 2.3 and 2.2, respectively, versus 2.6 at Filoha. If females in larger units spend more time in female-female interactions than females in smaller units do, then social interactions among females would be less frequent in a population with smaller units (Erer-Gota and Awash Station) than in a population with larger units (Filoha). Differences in demographic structure may thus partially account for the differences between my results and previous findings with regard to social interactions among females. Also contributing to the observed differences may be the fact that this was the first study to focus specifically on female-female social interactions in wild hamadryas baboons. Female behavior in hamadryas society is far less obvious than that of males, and interactions among females may be easily overlooked if they are not the explicit focus of observations.

Alternatively, there may be differences in food availability and distribution at each site that may lead to differences in female competitive regimes, which may account for differences in affiliative interactions among females. Consistent with previous studies of wild hamadryas, however, the Filoha females did not appear to compete directly over food. In this regard, they are similar to mountain baboons, which also feed on relatively scarce, widely dispersed food resources and whose females appear to engage in little or no feeding competition (Barton *et al.*, 1996; Byrne *et al.*, 1989). Unlike mountain baboons, however, which can be ordered into linear dominance hierarchies (Byrne *et al.*, 1989), the Filoha females showed no indication of dominance relationships. When agonistic interactions among Filoha females occurred, they were usually over grooming access to the leader male and were largely undecided. Competition for social access to males accompanied by an irresolution to agonistic interactions also occurs among female mountain gorillas (*Gorilla gorilla beringei*), which, like hamadryas, live in one-male groups and are dependent on males, rather than females, for protection and support (Watts, 1994a). Watts (1994a,b) suggested that, in gorillas, the fitness

benefits of bonds with males outweigh the fitness benefits of food competition with other females. This may be the case for hamadryas baboons as well.

Females in this study varied widely in their tendency to interact with other females. The factor most strongly associated with this variation was the number of females in a unit. Although hamadryas bands are large, cohesive social groups analogous to those of other baboon taxa, the herding behavior of hamadryas males divides the group into smaller units and inhibits social contact among their adult members. Thus, each adult's social options are essentially limited to other individuals within the one-male unit and the number of potential social interactants for each female is therefore largely determined by the size of her unit.

Beyond that explained by unit size, though, what might account for variation among females? It appeared that certain females (and dyads) simply had a greater intrinsic motivation to develop and to maintain female-female social relationships than did others. Differences among dyads in motivation to interact socially may be a function of kinship. In other baboon populations, related females spend more time grooming one another than do unrelated females (Saunders, 1988; Silk *et al.*, 1999; Walters, 1981). Among mountain gorillas, which, like hamadryas, live in one-male groups between which female transfers occur, maternally related females interact affiliatively more often and aggressively less often than do unrelated females (Watts, 1994b). An association between social interaction and kinship characterizes many other primate taxa as well (Gouzoules and Gouzoules, 1987).

Although genetic data for Filoha females are not available, microsatellite data from a nearby hamadryas group show a higher level of relatedness among females than typically exists for the dispersing sex in other taxa (Woolley-Barker, 1998, 1999). Accordingly, hamadryas females may have higher levels of intragroup relatedness and lower levels of dispersal than has been assumed, and females that interact the most may be half siblings or mother-daughter pairs. Related females might end up in the same unit through an expression of female choice on takeovers (Abegglen, 1984; Bachmann and Kummer, 1980; Swedell, 2000b), through a regular transfer of females between specific units due to a relationship between their leader males (Abegglen, 1984), or simply by chance. Sigg *et al.* (1982) reported that at Erer-Gota, females born into the same one-male unit often end up in the same unit as adults, and female relatedness reportedly influences unit membership among the free-ranging hamadryas of the Gumista Primate Reserve in Georgia as well (Chalyan *et al.*, 1994). Because of the forced transfer of females between one-male units and the rarity of social interaction among them, long-term relationships among females, regardless of whether they are based on kinship, cannot develop to the extent that they do in other baboons.

These relationships, however, especially if they are based on kinship, may be strong enough to endure periods of separation and to be continued when two females are reunited in the same unit after having been separated for lengthy periods of time.

If related females do not end up in the same one-male unit, they may cross unit boundaries to interact. Chalyan *et al*. (1994) observed that most free-ranging hamadryas females that crossed unit boundaries to groom one another were relatives, and Abegglen's (1984) observations also suggest that females attempt to interact with female relatives from which they have been separated by unit transfers. This may also be the case for the instances of inter-unit grooming at Filoha. If so, then this would suggest that the importance of female social bonds, regardless of whether they are based on kinship, outweighs the potential risk of aggression from a female's leader male.

Hypothesis #1: Do Filoha Hamadryas Conform to the Star-Shaped Sociogram?

These results do not support the hypothesis that hamadryas one-male units are characterized by a star-shaped sociogram (Colmenares *et al.*, 1994; Kummer, 1968). While Kummer's (1968) sociograms can be interpreted as having a star-shaped pattern, such a pattern does not characterize most one-male units in the Filoha population (Fig. 2).

That females spent more time with other females than would be expected based on the star-shaped model does not mean, however, that relationships among females are more important than those between each female and her leader male. Average percentages of time spent with the other females (Fig. 1) obscure the fact that this time is split among the other females in the unit, whereas percentages of time spent with the leader male reflect just that: time spent with the leader male. In Fig. 3, the positive correlations between unit size and a female's frequency of interaction with other females are much stronger than the respective negative correlations between unit size and a female's frequency of interaction with her leader male. This suggests that, as unit size increases, females increase their frequency of interaction with other females but do not necessarily decrease their frequency of interaction with the leader male to the same degree. Finally, females spent, on average, about as much time with their leader male but less time with each other female than would be expected based on pure social availability. Thus, despite their high rate of interaction with other females, Filoha females can be characterized as cross-bonded in that, for most of them, their most important social bond is with their leader male.

Hypothesis #2: Do Filoha Hamadryas Conform to the Non-Female-Bonded Model?

These results provide only partial support for the hypothesis that hamadryas baboons are a non-female-bonded taxon. Models of primate socioecology (Barton *et al.*, 1996; Sterck *et al.*, 1997; van Schaik, 1989; Wrangham, 1980) appear to correctly predict the patterning of agonistic, but not affiliative, relationships among hamadryas females. Consistent with previous reports on wild hamadryas baboons (Kummer, 1968; Sigg, 1980), I found no evidence of contest competition over food or dominance relationships among females. In contrast to previous reports, however, Filoha females interacted with other females at a higher rate than might be predicted by a socioecological model and cannot be accurately characterized as being non-female-bonded.

Byrne *et al.* (1989) and Barton *et al.* (1996) described some populations of chacma baboons as being cross-bonded in addition to (or instead of) being female-bonded. Although hamadryas males are clearly less flexible behaviorally than chacma males, as shown by their behavioral consistency regardless of environment (Kummer and Kurt, 1965), hamadryas females appear to be more flexible behaviorally and more similar to chacma females in that they may be both cross-bonded to their leader males and, to some extent, female-bonded as well. In hamadryas, as in chacma baboons, cross-bonding and female-bonding may not be mutually exclusive (Byrne *et al.*, 1989; Henzi *et al.*, 2000; Silk *et al.*, 1999).

The Evolution of Female Social Behavior in Hamadryas Baboons

Genetic evidence suggests that chacma baboons are the evolutionary outgroup to all other baboons (Newman *et al.*, unpubl. ms.; Newman and Rogers, 1999). Most, if not all, chacma populations conform generally to Wrangham's (1980) classic model of female-bonding (Byrne *et al.*, 1989; Henzi *et al.*, 2000; Silk *et al.*, 1999). Therefore, it is likely that the common ancestor to all extant baboons was female-bonded, or at least had the flexibility to be female-bonded depending on ecological circumstances. If so, then the multilevel social structure, male philopatry, and suite of traits characteristic of hamadryas baboons are derived in comparison and were probably selected for in response to the arid, semidesert climate and scarcity of food resources in the habitats in which hamadryas evolved (Dunbar, 1988; Jolly, 1963, 1993; Kummer, 1968, 1990, 1995). Barton *et al.* (1996) and Barton (2001) suggested that such a habitat, obviating the need for contest competition over food, would have given females no reason to form strong

and differentiated relationships with one another, leading ultimately to a lack of cohesion among females and a non-female-bonded social organization. Evidence from this study, however, suggests that the motivation and ability of females to form differentiated affiliative relationships with other females was not completely, or perhaps not at all, lost during the evolution of hamadryas baboons from their (presumably) female-bonded ancestors. Abegglen (1984) suggested that a female lineage system still exists in hamadryas baboons but that it has simply been fragmented by the behavior of males, who herd females out of their natal units and break up female kin bonds in the process. While hamadryas males are probably evolutionarily committed to their suite of derived, stereotypical behavioral traits (including herding, formalized notifications, and the motivation to form permanent one-male units), hamadryas females probably still retain the flexibility in social behavior and motivation to form affiliative relationships with other females that likely characterized the ancestral *Papio* baboon (Kummer *et al.*, 1970). Female bonding among hamadryas baboons may simply have been constrained during their evolutionary history by the development of herding behavior and the rigid, male-driven hamadryas social structure. Accordingly, ecological factors may be necessary but not sufficient to produce the apparent weakening of female bonds in hamadryas compared to other baboons, and the hamadryas pattern likely reflects a change in male behavior rather than a change in female behavior during the evolution of hamadryas social organization (Kummer, 1971; Kummer *et al.*, 1970). A female hamadryas baboon may not fully exercise her capacity for choice in unit membership – or may often choose to associate with a particular leader male rather than to remain with her female relatives – because maintaining a strong bond with a protective leader male is likely the main factor contributing to her reproductive success.

Cords, Clifford Jolly, Peter Henzi, Robert Seyfarth, Robin Dunbar, and two anonymous reviewers for valuable comments on the manuscript and to Eric Sargis for invaluable support.

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