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## **The Fourth Level of Social Structure in a Multi-level Society: Ecological & Social Functions of Clans in Hamadryas Baboons**

Amy Schreier  
*Regis University*

Larissa Swedell  
*CUNY Queens College*

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## RESEARCH ARTICLE

## The Fourth Level of Social Structure in a Multi-Level Society: Ecological and Social Functions of Clans in Hamadryas Baboons

AMY L. SCHREIER<sup>1,2\*</sup> AND LARISSA SWEDELL<sup>2,3</sup><sup>1</sup>Department of Evolutionary Anthropology, Duke University, Durham, North Carolina<sup>2</sup>New York Consortium in Evolutionary Primatology, New York, New York<sup>3</sup>Department of Anthropology, Queens College, City University of New York, Flushing, New York

Hamadryas baboons are known for their complex, multi-level social structure consisting of troops, bands, and one-male units (OMUs) [Kummer, 1968. *Social organization of hamadryas baboons*. Chicago: The University of Chicago Press. 189p]. Abegglen [1984. *On socialization in hamadryas baboons: a field study*. Lewisburg, PA: Bucknell University Press. 207p.] observed a fourth level of social structure comprising several OMUs that rested near one another on sleeping cliffs, traveled most closely together during daily foraging, and sometimes traveled as subgroups independently from the rest of the band. Abegglen called these associations “clans” and suggested that they consisted of related males. Here we confirm the existence of clans in a second wild hamadryas population, a band of about 200 baboons at the Filoha site in lowland Ethiopia. During all-day follows from December 1997 through September 1998 and March 2005 through February 2006, data were collected on activity patterns, social interactions, nearest neighbors, band fissions, and takeovers. Association indices were computed for each dyad of leader males, and results of cluster analyses indicated that in each of the two observation periods this band comprised two large clans ranging in size from 7 to 13 OMUs. All band fissions occurred along clan lines, and most takeovers involved the transfer of females within the same clan. Our results support the notion that clans provide an additional level of flexibility to deal with the sparse distribution of resources in hamadryas habitats. The large clan sizes at Filoha may simply be the largest size that the band can split into and still obtain enough food during periods of food scarcity. Our results also suggest that both male and female relationships play a role in the social cohesion of clans and that males exchange females within clans but not between them. *Am. J. Primatol.* 71:948–955, 2009. © 2009 Wiley-Liss, Inc.

**Key words:** hamadryas baboons; clans; spatial association; multi-level social structure

## INTRODUCTION

Hamadryas baboons (*Papio hamadryas hamadryas*) are known for their unique multi-level social structure in which large groups break into smaller foraging parties during daily travel. It is thought that this nested social structure is related to the sparse distribution of resources in hamadryas habitats and allows a large group to break up during daily travel so that all group members can obtain sufficient food resources [Kummer, 1968, 1971, 1995].

Three main levels of organization characterize hamadryas society. *Troops* are large groups (up to several hundred baboons) that assemble at sleeping cliffs, but otherwise do not function as unified social groups. Each troop consists of 1 or more *bands*, stable social units that usually travel together during the day, coordinate their overall movements and activities, and sleep on the same cliff each night. The band is analogous to the “troop” in other *Papio* baboons, and hamadryas social interactions as a whole occur almost exclusively among members of

the same band. The band comprises a number of *one-male units* (OMUs), each consisting of a leader male, several females, their dependent offspring, and occasionally one or more “follower” males. There also exist solitary males, males that are not asso-

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\*Correspondence to: Amy L. Schreier, Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC 27708. E-mail: as243@duke.edu

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ciated with any particular OMU but associate mainly with other solitary males throughout the band [Swedell et al., 2008b]. OMUs, though not solitary males, are socially and spatially cohesive, and most social interactions among females occur within OMUs rather than among them [Abegglen, 1984; Kummer, 1968, 1971; Swedell, 2002a, 2006]. Leader males also typically do not interact with individuals outside of their OMU.

Abegglen [1984] was the first to document a fourth level of social organization in hamadryas society, which he called "clans." Abegglen noticed that certain OMUs and solitary males in the Erer-Gota population in Ethiopia rested near one another on the sleeping cliff, traveled together during the day, and occasionally traveled as subgroups independently from the rest of the band. Based on physical resemblance among males, he suggested that these associations of OMUs and solitary males consisted of male relatives.

Although clans have been described for two bands at Erer-Gota [Abegglen, 1984; Kummer, 1995; Sigg & Stolba, 1981; Sigg et al., 1982], they have not been identified in any other wild population to date [Saudi Arabia: Biquand et al., 1992; Kummer et al., 1985; Mori et al., 2007; Eritrea: Zinner et al., 2001]. A clan structure has been described for captive hamadryas baboons in the Madrid Zoo Colony [Colmenares, 1992, 2004; Colmenares et al., 2006], though this population includes hybrids (*P. hamadryas hamadryas* × *P. hamadryas cynocephalus*) and is obviously somewhat constrained in its patterns of aggregation and cohesion due to captivity. Abegglen's supposition that clans consisted of related males was never tested with genetic evidence for the Erer-Gota population, but clans in the captive Madrid colony have been shown to consist only of related males [Colmenares, 1992; Colmenares et al., 2006].

In this article, using patterns of spatial association among males, we report evidence for the clan level of social structure in a second population of wild hamadryas baboons in Ethiopia. The relative spatial arrangement of animals has been shown to reflect their social organization [Kummer, 1968; Whitehead, 1997], and spatial data can be used to represent patterns of interactions among members of a social group [Whitehead & Dufault, 1999]. Observations of associations of individuals in space have been used to quantify social structure across a wide range of primate taxa [pygmy chimpanzees, *Pan paniscus*: White & Burgman, 1990; proboscis monkeys, *Nasalis larvatus*: Yaeger, 1990; spider monkeys, *Ateles belzebuth belzebuth*: Shimooka, 2003; howler monkeys, *Alouatta palliata*: Dias & Luna, 2006; Lemurs, *Lemur catta*, *Eulemur fulvus*, *Eulemur coronatus*: Kappeler, 1993], including baboons [chacma baboons, *Papio ursinus*: Byrne et al., 1989; hamadryas baboons, *P. hamadryas hamadryas*:

Colmenares et al., 2006; Mori et al., 2007]. Here we use spatial associations among leader males as evidence for the existence of clans in a band of free-ranging hamadryas baboons in central Ethiopia. In addition, we discuss the possible functions of clans in this population as well as the roles of both males and females in maintaining clan social cohesion.

## METHODS

### Study Site and Subjects

This study took place at the Filoha outpost of the Awash National Park, Ethiopia (9°6'27"N, 40°0'50"E) over two observation periods: (1) December 1997–September 1998 (L. S.) and (2) March 2005–February 2006 (A. S.). The outpost is surrounded by about 2 km<sup>2</sup> of natural hot springs, doum palm trees (*Hyphaene thebaica*), swamp vegetation, and a 1.5 km-long cliff [Swedell, 2002b, 2006]. The surrounding area of *Acacia* scrubland and open grassland is characteristic of hamadryas habitat in many other areas of their range. Several bands of hamadryas baboons populate the Filoha region, and sleep on the Filoha cliff as well as another cliff (Wasaro) 4 km from Filoha.

Band 1 has been the focus of studies intermittently since 1996 [previously called "Group 1": Swedell, 2000, 2002a, 2002b, 2006; Swedell & Tesfaye, 2003]. In April 1998, Band 1 consisted of about 175 individuals, including 24 leader males, 5 follower males, about 10 subadult males, 46 adult females, and at least 80 juveniles and infants [Swedell, 2006]. In February 2006, Band 1 consisted of approximately 210 individuals, including 24 leader males, 7 follower males, about 20 adult and subadult solitary males, 53 adult females, 13 subadult females, and at least 90 juveniles and infants. All adult and subadult females were members of OMUs. Leader males, adult females, and subadult females were recognized individually, but the identities of most follower males, solitary males, and juveniles were unknown. Age classes were estimated following Sigg et al. [1982] and Swedell [2006]. Because observations between 1998 and 2002 were intermittent and not all individuals in Band 1 were known or monitored during this period (and this population is not marked or tagged), an unknown number of the individuals in the 2005–2006 study period are likely the same, but with different names, as those in 1997–1998.

### Data Collection and Analyses

Data on activity patterns, habitat use, and social and spatial cohesion derive from all-day follows of Band 1. The baboons were located at their sleeping cliff at 0600 hr and were followed until 1800 hr, or for as long as possible until they had to be left in order to arrive at camp by dark. During all-day follows, we conducted scan samples of known OMUs to measure

spatial cohesion and social interaction. During the 1997–1998 observation period, L. S. conducted instantaneous scan samples of OMUs at 10-minute intervals, during which the activities of leader males and all adult and subadult females were recorded [Altmann, 1974]. As a measure of association among OMUs, the identity of the leader male of the nearest other OMU was recorded during each scan. During the 2005–2006 observation period, A. S. conducted instantaneous scan samples at 2-minute intervals during 30-minute focal samples of individual OMUs. To increase inter-sample independence and comparability of the two data sets, only scans separated by 10 min were used in these analyses. In each scan sample, the activity of each adult and subadult member of the OMU was recorded. To measure spatial cohesion among OMUs, the number of OMUs within a 10 m radius of the leader male of the focal OMU was counted, and the identity of each other leader male was recorded.

With the 1997–1998 data, for each leader male we calculated the number of scans that each other leader male was his nearest neighbor, and the samples in which male A was male B's nearest neighbor were pooled with the samples in which male B was male A's nearest neighbor. Analyses are based on the 16 leader males for whom nearest-neighbor data exist (Table I). With the 2005–2006 data, for each leader male we calculated the number of times that each other leader male was within a 10 m radius of him, and the samples in which male A was within 10 m of male B were pooled with the samples in which male B was within 10 m of male A. In an effort to measure associations and relationships that were consistent over time, these analyses are based on 22 males that were leader males for at least 8 consecutive months (Table II). The data sets

**TABLE I. Leader Males Included in Analyses, 1997–1998 Observation Period**

Leader male	Number of scans
Al	57
Bo	29
Da	93
Em	38
Ha	86
Ik	63
Ju	78
Ke	11
Leo	40
Max	46
Ni	17
Or	63
Ru	34
Se	70
Xi	29
Ze	10
Total scans	764

from both observation periods include scans during which the baboons rested and groomed on sleeping cliffs as well as scans during which they foraged during daily travel (1997–1998:  $N = 764$ ; 2005–2006:  $N = 1942$ ).

Association indices were computed for each dyad of leader males via the half-weight index [Cairns & Schwager, 1987], which accounts for differences among individuals in number of observations:  $I_{AB} = AB/A+B$ .  $I_{AB}$  is the dyadic association index for dyad AB; AB is the number of scans in which A and B were nearest neighbors (1997–1998) or in which A and B were within a 10 m radius of one another (2005–2006); A is the total number of scans for A; and B is the total number of scans for B. Association data were analyzed by hierarchical cluster analysis, using the complete-linkage method and Euclidean distances [e.g. De Gheff, 1978; Morgan et al., 1976; Whitehead & Dufault, 1999]. Analyses were performed using Statistica 6 software (StatSoft, Inc., Tulsa, OK).

Because cluster analysis is a descriptive method, the number of true clusters in a data set is often unclear [Dudoit & Fridlyand, 2002; Tibshirani et al., 2001]. We used the gap statistic, therefore, to validate the number of clusters in the data [Tibshirani et al., 2001]. The gap statistic uses the output from any clustering algorithm and compares the change in within-cluster dispersion ( $W_k$ ) to that expected under a null distribution. The optimal number of clusters, then, is the value of  $k$  for which

**TABLE II. Leader Males Included in Analyses, 2005–2006 Observation Period**

Leader male	Number of scans
An	124
Cl	106
Co	123
Dj	52
Ev	71
Fo	47
He	103
Ka	124
Len	72
Mac	64
Mi	93
Ne	43
Pa	41
Pea	101
Pet	95
Re	106
Sa	91
Sh	87
Te	75
Ti	71
Tr	110
Yi	143
Total scans	1942

$\log(W_k)$  falls farthest below the reference curve. The gap test was performed using Mathematica 6 software (Wolfram Research, Inc., Champaign, IL).

During the 2005–2006 study period, Band 1 fissioned several times, and OMU membership for each subgroup within the band was recorded during each band fission. During both study periods, observations of interactions across OMU boundaries and those surrounding takeovers were made during focal samples on females (1997–1998) and OMUs (2005–2006) as well as on an ad libitum basis [Altmann, 1974].

This research adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates, and protocols were approved by the Queens College Institutional Animal Care and Use Committee (L. Swedell, Protocol 93).

## RESULTS

### Spatial Associations Among OMUs

The resulting dendrograms of the cluster analyses indicate a clear pattern of spatial organization among OMUs, as reflected by association among leader males. The dendrogram for the 1997–1998 period ( $N = 764$ ) displays two main subgroups of 9 and 7 OMUs, respectively (Fig. 1). As groups of OMUs that associate more frequently with certain other OMUs, these subgroups represent clans. The subset of 9 OMUs on the left side of the dendrogram was termed Clan 1, within which we identified three clusters of 2–4 OMUs each. The subgroup of seven males on the right side of the dendrogram was termed Clan 2, and consisted of two subsets of OMUs, with 2 and 3 OMUs respectively, as well as 2 OMUs that did not cluster more closely with any of the other OMUs in the clan. The gap statistic indicated that there was just one cluster in the

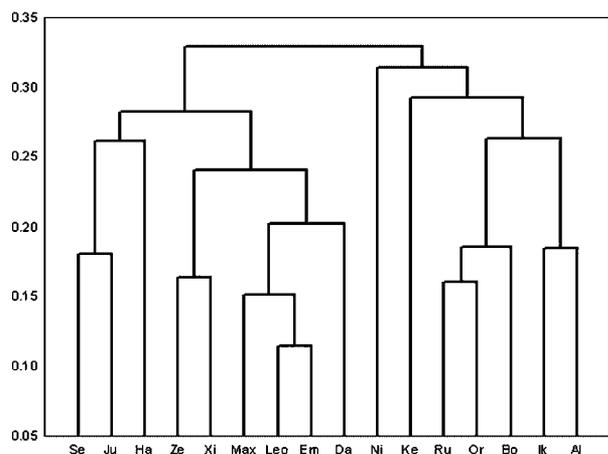


Fig. 1. Complete-linkage cluster analyses of association indices among leader males during the 1997–1998 observation period ( $N = 764$ ). Association indices based on the number of scans in which two leader males were each other's nearest neighbors. X-axis = leader males; Y-axis = linkage distance. Stronger clusters are lower in the figure.

1997–1998 data set (i.e. clusters did not exist), likely due to the relatively small size of this data set.

Clan membership in 1997–1998 appeared to correspond well with observed positions of OMUs on the Filoha sleeping cliff just before dark. To the extent that positions on the sleeping cliff were recorded, these data suggest that the OMUs of the leader males Da, Ha, Leo, Max, and Xi (i.e. members of Clan 1) consistently slept on the southern portion of the cliff (south of a walkway regularly used by humans) and the OMUs of the leader males Al, Bo, Ik, Or, and Ru (i.e. members of Clan 2) consistently slept on the northern portion of the cliff (north of the walkway).

Results of the cluster analyses from the 2005–2006 observation period also reveal two clans. The dendrogram shown in Figure 2 ( $N = 1942$ ) displays two main subgroups of 13 and 9 OMUs, respectively. The subset of 13 OMUs on the left side of the dendrogram was termed Clan A, and included three subsets of 2, 5, and 6 OMUs. The subgroup of nine males on the right side of the dendrogram was termed Clan B, and also consisted of three smaller subsets of OMUs, with 3 OMUs each. The results of the gap test verified the existence of two clusters with 13 and 9 OMUs each. To further test the robustness of the observed clusters, we redid the cluster analyses by omitting each individual male as well as 20 random pairs of males. For the 2005–2006 data set, the two clusters remained the same when each individual male was omitted from the analysis, as well as in all 20 cases in which different pairs of males were omitted from the analysis.

### Temporary Fissions into Clans

Band 1 separated for periods of 3 hr to 31 days at a time during the 2005–2006 study period, and these

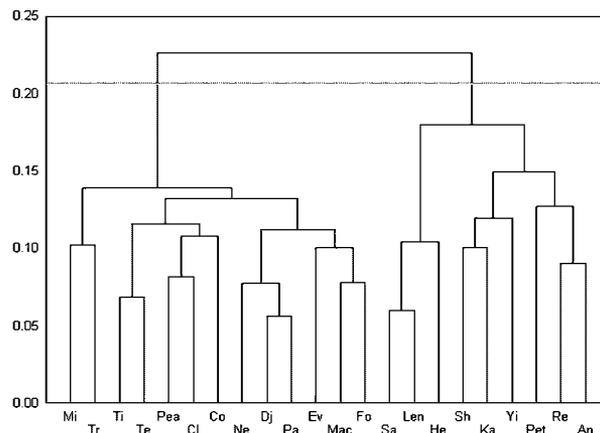


Fig. 2. Complete-linkage cluster analyses of association indices among leader males during the 2005–2006 observation period ( $N = 1942$ ). Association indices based on the number of scans in which two leader males were within a 10 m radius of one another. X-axis = leader males; Y-axis = linkage distance. Stronger clusters are lower in the figure. The dotted line cuts the tree, leaving two clusters as suggested by the gap statistic.

separations were always along clan lines (as identified by the analyses reported here). The first such temporary fission occurred for 6 consecutive days in March. The OMU composition of subgroups during this fission corresponded to that of Clan A and Clan B described above. Of the 17 males who were leader males throughout the study period, only one OMU traveled with the opposite clan during the March fission. The second temporary fission, lasting at least 31 days in September and October, also occurred along clan lines. In addition to these extended separations, Band 1 separated along clan lines for a minimum of 3 hr during daily travel on at least 9 days (out of 105 days).

### Takeovers and Clan Membership

Only one takeover was observed during the 1997–1998 observation period [Swedell, 2000, 2006]. Of a leader male's five females, three were taken over by three other leader males in Band 1; one was taken over by a solitary male; and one was not seen again [Swedell, 2000]. All leader males known to be involved in this takeover were members of Clan 1.

During the 2005–2006 study period, three takeovers were observed. In two cases leader males lost their females to other males from Band 1. The results of the cluster analyses and OMU composition during band fissions indicate that both males involved in each takeover belonged to the same clan. In the third takeover, a leader male's three females joined another OMU in Band 1 after he disappeared. Both the previous and new leader male involved in this takeover were from Clan B.

### Extra-OMU Interactions

The primary grooming partners of leader males were females in their own OMUs, and no leader male was ever observed grooming with a member of another OMU (either another leader male or his females). Leader males did occasionally groom with other males (solitary and follower males), but this occurred in less than 5% of the total number of scans in which they were observed grooming over the two study periods (1997–1998:  $N = 422$ ; 2005–2006:  $N = 1839$ ). As the identities of nonleader males were not known, whether these male grooming partners were members of the same clan couldn't be addressed.

Adult and subadult females were observed interacting across OMU boundaries 13 times during the 1997–1998 study period and 17 times during the 2005–2006 study period. These female–female interactions consisted of presenting, genital inspecting, infant inspecting, sitting close (within 10 cm), or grooming. Of the 13 extra-OMU interactions in 1997–1998, 12 occurred between females in the same clan. Of the 17 such interactions in

2005–2006, all occurred between females belonging to the same clan.

## DISCUSSION

### Clans at Filoha

The results of cluster analyses show that Band 1 at Filoha is divided into two distinct units based on spatial associations among males and social interactions among females. The division into two clans characterized both the 1997–1998 and the 2005–2006 study periods. The gap statistic, an additional test used to verify cluster analyses, confirmed the existence of the two clusters in the 2005–2006 data set, but indicated just one cluster for the 1997–1998 data set. This is likely due to the relatively small sample size during the earlier observation period. When sample sizes are small the gap statistic tends to be biased downwards, selecting only one cluster even when cluster analyses show clusters in the data set [Tibshirani et al., 2001], as is the case here. Thus, we posit that the gap statistic would have confirmed the results of the cluster analysis with a larger data set. As it stands, our results validate the existence of two clusters in 2005–2006 and are suggestive of two clusters in 1997–1998.

Following previous descriptions of hamadryas social organization at Erer-Gota [Sigg et al., 1982; Abegglen, 1984], we interpret these two groupings in Band 1 to be clans. Similar to the clans described for the Erer-Gota population, OMUs within each clan at Filoha rested near one another on sleeping cliffs, foraged together during daily travel, and sometimes traveled independently from the rest of the band.

The sizes of the clans at Filoha, however, differ from those described elsewhere. Band I at Erer-Gota consisted of three clans, with 2, 3, and 4 OMUs respectively [Abegglen, 1984], and clans in the captive Madrid colony also comprise between 2 and 4 OMUs [Colmenares, 1992; Colmenares et al., 2006]. Band 1 at Filoha, by contrast, was composed of two large clans with 13 and 9 OMUs in 2005–2006, and two likely clans of 9 and 7 OMUs in 1997–1998. (Although smaller subgroupings of two, three, or four males existed within the two large clusters, they were not consistent across analyses.) Large clan size, therefore, appears to be a characteristic of the Filoha population.

The larger number of OMUs per clan at Filoha may relate to both larger band sizes and differing patterns of food availability at Filoha compared with other hamadryas sites. The band sizes in the Filoha population of hamadryas baboons are larger than those described for other populations [Erer-Gota, Ethiopia: Abegglen, 1984; Kummer, 1968; Sigg & Stolba, 1981; Awash River, Ethiopia: Kummer et al., 1981; Nagel, 1973; Saudi Arabia: Biquand et al., 1992; Yemen: Al-Safadi, 1994], and this is likely related to the high abundance of doum palm fruit

(*H. thebaica*), a preferred food item, at Filoha [Swedell, 2002b, 2006; Swedell et al., 2008a]. It is possible, therefore, that the availability and distribution of palm trees in the Filoha area allow both larger band sizes and larger clan sizes at Filoha compared with elsewhere. There is some evidence to suggest that baboons at Filoha need not split up into smaller groupings when foraging on palm fruit, even though they may do so when foraging in *Acacia* thorn scrub. For example, Schreier [2009] reported significantly fewer OMUs within a 10 m radius when foraging in *Acacia* scrublands compared with palm forests, with leader males remaining in closer proximity to one another in palm forests compared with *Acacia* scrublands, suggesting that, overall, Band 1 foraged more often as individual OMUs in *Acacia* scrublands but more often as clans in palm forests. The clan sizes at Filoha may thus correspond to the amount of food available within a single palm forest.

### Functions of Clans

Previous research has suggested two possible, and potentially overlapping, functions of the clan layer of the hamadryas social system. The first possibility is that clans simply provide an additional cleavage point for band subdivision during daily travel, thereby enabling greater foraging flexibility and increased access to widely dispersed and limited food resources. The second possibility is that the clan structure reflects male–male relationships and philopatry in that males within clans are more closely related, more strongly bonded, and better able to cooperate over access to and control of females [Abegglen, 1984; Kummer, 1995]. Our results support both of these hypotheses.

The multi-level social structure of hamadryas baboons has been attributed to the sparse distribution of resources in their habitats: coming together as troops at sleeping sites provides necessary protection from predators, while separating into OMUs during the day enables the baboons to find sufficient food [Kummer, 1968, 1971, 1995]. Despite the apparent abundance of food resources at Filoha (i.e. the presence of doum palms) compared with other areas inhabited by hamadryas baboons, periods of relative food scarcity may underlie band fissions into clans for extended periods. During the 2005–2006 study period, doum palm fruit made up 20% of Band 1's annual diet, second only to *Acacia senegal* (23%) [Schreier, 2009]. Palm fruit contribution to monthly diets corresponded to its seasonal availability, comprising over 20% of the monthly diet during 7 months of the year, but less than 5% of the diet in both September and October when ripe doum palm fruit was not available throughout Band 1's home range [Schreier, 2009]. September and October were also the months when Band 1 spent the longest period of time separated into clans. It is possible,

therefore, that Clan A and Clan B functioned as independent subgroups during this period of low palm fruit availability as a means of avoiding feeding competition. Additionally, a peak in births occurred during this period. Of 32 births over the study period, 9 occurred between 30 September and 10 October [Schreier, 2009]. Traveling as independent clans may thus have enabled females to obtain sufficient nutrition during the critical first days of an infant's life. Lastly, all 9 days that the baboons separated along clan lines for at least 3 hr during daily travel occurred during the dry season when fresh *A. senegal* flowers, leaves, and pods were scarce [Schreier, 2009]. The ability to fission into clans, therefore, seems to provide an extra level of flexibility during periods of relative resource scarcity.

As mentioned above, the presence of doum palms in the Filoha region appears to allow larger band sizes than elsewhere due to greater food abundance. The consequence of this, however, is that during periods of low abundance of palms, bands are too large to subsist on the predominantly *Acacia* thorn scrub and must split into clans for longer periods of time in order to obtain enough food. During these periods, *clans* at Filoha may fill the ecological role of *bands* in other areas of hamadryas range that are dominated by thorn scrub and where doum palms are not present. The clan sizes at Filoha (Clan A = ~100 baboons, Clan B = ~84 baboons) are comparable to the band sizes of 62–95 individuals at Erer-Gota [Abegglen, 1984; Sigg & Stolba, 1981], suggesting that this is an adaptive group size in a thorn scrub habitat.

Abegglen [1984] suggested that clans consisted of related males and reported that social interaction among males occurred more frequently among males in the same clan than among males without this association. Colmenares [1992] reported that clans in the captive Madrid colony consisted only of related males and that the strongest associations occurred between fathers and sons, as well as between half-brothers sharing the same mother. Clan males in this colony had greater success taking over females [Colmenares et al., 2006], longer tenures as leader males, and larger OMUs than leader males who led single OMUs not belonging to a clan [Colmenares, 1997].

Although we do not yet have genetic data to assess kin relationships among clan males at Filoha, behavioral evidence suggests that takeovers are more likely between males belonging to the same clan. All males and females involved in the takeovers described above for the 2005–2006 period, and likely the 1997–1998 takeover as well, remained in the same clan before and after the takeover. It thus appears that relationships among males in the same clan facilitate access to and exchange of females. Future research on relationships among leader, follower, and solitary males, currently in progress,

should elucidate the social and kin bonds among males that underlie these patterns.

It has also been reported that female kinship and familiarity facilitate the existence of clans [Colmenares, 1992]. In other populations, females who once belonged to the same OMU tend to reunite later in life in new OMUs [Abegglen, 1984]. In captivity, related females or those that have been members of the same OMU for many years tend to interact with one another even if they no longer belong to the same OMU [Colmenares, 1992]. At Filoha, virtually all extra-OMU interactions occurred between females belonging to the same clan. Although available data do not allow us to determine whether these pairs of females belonged to the same OMU earlier in life or were close relatives, the tendency of takeovers to occur between OMUs in the same clan suggests that this is possible. Female relationships also appeared to play a role in one of the takeovers in 2005. In this takeover, the new leader male did not exhibit the neck-biting and aggressive herding that is typical of hamadryas males during takeovers of females [Swedell & Schreier, 2009]. Instead, the females' entry into his OMU appeared to be based on their relationship with the leader male's previous original female. Future genetic analyses will reveal whether pairs of females such as these—as well as those that interact across OMUs—are close relatives.

In summary, Band 1 at Filoha comprised two clans, consisting of 9 and 7 OMUs in 1997–1998 and 13 and 9 OMUs in 2005–2006. The large clans at Filoha appear to be related to both band size and the availability and distribution of palm fruits: clans may simply be the largest size that the band can split into and still get enough food during periods of palm fruit scarcity. Clans at Filoha, therefore, appear to provide an extra level of flexibility to avoid feeding competition during periods of low food availability. In addition, behavioral evidence suggests that takeovers occur mainly among males belonging to the same clan, and that female social relationships, and perhaps kinship, also play a role in clan membership. Future research on the roles and reproductive success of follower and solitary males at Filoha should lend insight into the benefits that this fourth level of social structure affords male and female hamadryas baboons.

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