



Social System of a Hybrid Baboon Group (*Papio anubis* × *P. hamadryas*)

Thore J. Bergman^{1,3} and Jacinta C. Beehner²

Received November 13, 2003; revised February 11, 2004; accepted February 23, 2004

*We describe the social organization, mating system, and social structure of a group of hybrid baboons (*Papio anubis* × *P. hamadryas*) in Ethiopia's Awash National Park. The group contained elements of both hamadryas and anubis societies. Overall, the group was a multimale, multifemale group that lacked cohesion and frequently formed subgroups. Subgroup formation was more strongly associated with predation risk than food availability. Although there were several hamadryas-like one-male units OMUs within the group, there was no evidence of a hamadryas multilevel society. Male and female members of OMUs were phenotypically more hamadryas-like than non-OMU individuals. The group contained substantial variation in the strength of inter- and intrasexual bonds: some females primarily groomed males while other females primarily groomed females, and the patterns were consistent with the OMU substructure. Despite some promiscuous mating, mating was biased towards the hamadryas condition for all group members. Additionally, rates of immigration and emigration were very low, and mean pairwise relatedness within the group is rising. For measures of intersexual bonding, all members of the group were intermediate between anubis and hamadryas individuals in less hybridized groups. The group was phenotypically and behaviorally more intermediate than it was in the 1970s (Sugawara,*

¹Biology Department, Washington University, St. Louis, Missouri.

²Anthropology Department, Washington University, St. Louis, Missouri.

³To whom correspondence should be addressed at Department of Biology, Leidy Laboratories, University of Pennsylvania, Philadelphia, Pennsylvania 19140; e-mail: thore@sas.upenn.edu.

K. (1988). Primates 29: 429–448.) and the changes may indicate a relatively young and dynamic hybrid zone.

KEY WORDS: social organization; social structure; mating; baboon; hybrid; socioecology.

INTRODUCTION

In a recent review of the evolution of primate social systems, Kappeler and van Schaik (2002) emphasized that social systems consist of three distinct components: social organization, mating system, and social structure. Although interrelated, the three components deal with separate facets of social systems: the composition and stability of the social unit, the pattern of mating and its genetic consequences, and the social relationships within the social unit. We analyzed these three components in a group of hybrid baboons (*Papio anubis* × *P. hamadryas*) at the center of the baboon hybrid zone in Awash National Park, Ethiopia (Phillips-Conroy and Jolly, 1986).

The Awash hybrid zone has received considerable attention, primarily because the parental forms are divergent in all three elements of their social system (Nagel, 1973; Phillips-Conroy *et al.*, 1991; Phillips-Conroy and Jolly, 1986; Sugawara, 1982). The social organization of anubis consists of large, cohesive multimale, multifemale groups with no permanent substructuring (DeVore and Hall, 1965), while hamadryas live in a multilevel society characterized by tightly-bonded unimale, multifemale groups (one-male units or OMUs) that aggregate at multiple levels into clans, bands, and troops (Abegglen, 1984; Kummer, 1968a). Mating in anubis societies is promiscuous, with male competition for access to fertile females mediated by a strict dominance hierarchy (Packer, 1979b), while hamadryas have a harem polygynous mating system (Kummer, 1968a). In anubis groups, the strongest bonds among group members are within matrilineal natal females (Moore, 1978; Smuts, 1985), while the strongest bonds in hamadryas society are between a male and the females within the OMU (Kummer, 1968a).

Here, we describe the social organization, mating patterns, and social structure of the most phenotypically varied group in the Awash hybrid zone. Specifically, we asked whether elements of the social system from the group are anubis-like, hamadryas-like, or somewhere between the anubis and hamadryas conditions.

Next, we address how the group changed since a major description and evaluation more than two decades ago (Sugawara, 1979, 1982, 1988). While many of the data we report are new and are not from provisioned subjects,

we use Sugawara's data to document changes in group composition, group size, and general behavioral differences. We interpret the changes in relation to the dynamics of the hybrid zone.

METHODS

Study Group

Our data are from observation and analysis of members of a single group at the phenotypic center of the Awash hybrid zone, group H. The range of H extends approximately 3–8 km below the Awash Falls (Phillips-Conroy and Jolly, 1986). For more than 30 years, group members have spanned the phenotypic spectrum from anubis to hamadryas (Bergman, 2000; Nagel, 1973). Groups upstream of H are (and were) predominantly anubis (genetically and phenotypically), and those downstream are (and were) predominantly hamadryas (Bergman, 2000; Beyene, 1998; Nagel, 1973; Nystrom, 1992; Phillips-Conroy and Jolly, 1986). When sampled in 1973, H encompassed the greatest nuclear and mitochondrial genetic diversity of any surveyed group in the hybrid zone (Newman, 1997; Woolley-Barker, 1999), with a gene pool drawn equally from hamadryas and anubis ancestry. Similar genetic diversity existed during our study (Bergman, 2000). Over 10 mos between 1975 and 1979, Sugawara observed H as part of a socioecological comparison to a more hamadryas group downstream (Sugawara, 1979, 1982, 1988). We discuss his findings as we describe changes in the group since his study.

In documenting group membership, a male was considered an adult when dentally mature, with at least one-third molar erupted. Based on dental eruption schedules, adult males are approximately 98 mos old (Phillips-Conroy and Jolly, 1988). They showed adequate development of secondary sexual characteristics to determine the phenotypic hybrid index (PHI) score. A female was considered an adult after her first full-term pregnancy, (typically 6–7 yr). We observed a total of 30 adult females and 21 adult males.

Behavioral Observations

Data were collected from September 1997–November 1998 (TJB) and from December 1999–December 2000 (JCB). We collected daily observations on the formation of subgroups, male and female membership of subgroups, females in estrus and their consort partners. The principal

method of behavioral data collection was all-occurrence and scan sampling (Altmann, 1974). We attempted focal sampling, but ceased because the extremely rough terrain, poor visibility, and limited habituation of the group made it nearly impossible to observe the same individual for even short intervals. Therefore, we recorded social behaviors of interest via all-occurrence sampling and then standardized the data (for time spent observing each individual) by scan samples. We scanned the group every 5 min to keep a record of all individuals being observed and their nearest neighbors.

Structure of the Group

In defining long-term subunits within the group, we used nearest neighbor data and information on subgroup patterns. The group contained OMUs that were spatially-cohesive, discrete entities even in the context of the entire group, as in hamadryas societies (Kummer, 1968a). We were easily able to score membership in these OMUs on any given day. However, we also observed less cohesive groups that we called "loose OMUs" (Beehner and Bergman, in press). Loose OMUs were spatially less distinct than other OMUs (which, for clarity, will be called "strict OMUs"), and loose OMU members were often interspersed with nonmembers. Both strict OMU males and loose OMU males rarely showed aggressive herding behaviors towards their females. Unlike strict OMUs, loose OMUs were not immediately obvious and only after observing consistent membership and neighbor associations within the same subgroup, in addition to exclusive consortships between the same male and females, was it clear that the groups represented a third pattern of behavior in the substructure of H. Like strict OMU females, loose OMU females were always in consort with the leader male when in estrus, and membership in loose OMUs was consistent. For all OMUs, changes in membership were abrupt and obvious, particularly because interactions were most intense between an OMU male and a newly acquired female.

We use the general term OMUs to refer to both strict and loose OMUs, unless otherwise specified. When comparing PHI scores of OMU and non-OMU females, we removed females that changed OMU categories during the study from the analysis.

We also analyzed the formation of temporary subgroups (foraging parties). We recorded a foraging party and its members each time new members converged or split off from a focal group. The analysis of foraging party formation is restricted to 310 days when membership in subgroups could be assigned with confidence. As a measure of foraging party size, we used the percentage of adult males present because (1) males were the most likely to be identified and (2) nearly every subgroup contained at least one male.

The formation of smaller foraging parties may be an adaptation to foraging in a resource-poor environment because it allows an entire group to forage over a large area while minimizing individual travel distance (Aldrich-Blake *et al.*, 1971; Kummer, 1968b). In primates, rainfall is a major determinant of group size across habitats (Dunbar, 1988, 1996). Therefore, we analyzed foraging party size across seasons, hypothesizing that they would be smaller and more frequent during the dry season when resources were poor than during the wet season when resources were plentiful. Because plant biomass is significantly correlated with the previous 2 mos of rainfall (Dunbar *et al.*, 2002), we assessed wet and dry season months according to the previous 2 mos of rainfall. We categorized a mos as part of the wet season if >80 mm of rain fell in the previous 2 mos (Beehner, 2003).

Sugawara (1979) designed a method to analyze substructure within a group. He calculated a measure of overlap for each pair of males in the group via the following formula:

$$\text{foraging party overlap} = \frac{1000 \times N(A + B)}{N(A) + N(B)}$$

where in N represents the number of foraging parties in which male A or B or both were present. Theoretical values for the measure range from 0 (never together) to 500 (always together) and can be entered in a single-link cluster analysis to create a representation of grouping patterns. Clusters of males in the analysis indicate that they frequently form subgroups together and clusters of OMU males might suggest the presence of clans or bands in a hamadryas-like multilevel society (Abegglen, 1984). We repeated Sugawara's analysis using a subset of data from 1997–1998 when there was no change in the adult male membership of the group.

Ancestry

We evaluated a phenotypic measure of ancestry called the “hybrid index” (Nagel, 1973) though it is scaled to the typical anubis condition rather than to hybridity *per se*. We based the phenotypic hybrid index (PHI) on character states previously used to classify Awash baboons (Nagel, 1973; Phillips-Conroy and Jolly, 1986), with the addition of extra, intermediate states expressing finer degrees of physical intermediacy in hybrids (Bergman and Beehner, 2003). We scored four characters for males and females: face color, mane/hair color, mane/hair length, and tail shape. We scored an additional four characters in males: cheek tuft color, cheek tuft shape, anal patch shape, and anal patch skin color. In males, a score of 0.0 on each character represents the pure hamadryas state, scores of 0.5, 1.0 and 1.5 represent intermediate states, and a score of 2.0 represents the pure

anubis state. To make scores comparable to scores for males, scores for each character in females ranged from 0.0 (pure hamadryas state) to 4.0 (pure anubis state). We summed scores across characters, yielding a range from 0.0 for a pure hamadryas phenotype to 16.0 for a pure anubis. PHI scores in H ranged from 5.0 to 15.0 in males and from 4.0 to 16.0 in females. Although the genetic basis of the character states is unknown, the PHI may provide a good measure of individual ancestry (Nagel, 1973; Phillips-Conroy and Jolly, 1986). The characters sort independently (Nagel, 1973), are evenly weighted, and their extreme states are completely diagnostic. The PHI scores of likely F1 hybrid males are approximately 8.0 (Bergman and Beehner, 2003), as expected for individuals with equal hamadryas and anubis ancestry.

Relatedness

To analyze pairwise genetic relatedness, we collected DNA from over 90% of the members of H by trapping them in steel cages and releasing them 30 minutes later (Brett *et al.*, 1982). We purified DNA from blood (74 samples) or hair follicles (19 samples) via Qiagen extraction kits. We screened samples at 9 tetra-repeat microsatellite loci (amplified with human MapPair primers D2S1399, D3S1766, D4S243, D6S1280, D7S817, D11S2002, D12S375, D142306, and D19S716) that are all on different chromosomes in humans (Woolley-Barker, 1999). We PCR-amplified DNA via fluorescent-labeled primers with Perkin-Elmer Thermocycler 2400 or 9600s in a touchdown program under hot-start reaction conditions via heat-activated *AmpliTaq* Gold polymerase (Woolley-Barker, 1999). We electrophoresed samples via ABI 377 and 310 automatic sequencers using 4.0% denaturing gels or polymers visualized with GeneScan software (Applied Biosystems, Inc.). We included a size standard (TAMRA 500) in each lane and scored alleles manually. We analyzed all alleles at least twice and homozygotes three times. Were re-ran discrepancies until the same result was achieved three times consecutively or, failing that, we left them unscored (4.9% of alleles).

We calculated statistical estimates of pairwise interindividual relatedness using the Queller and Goodnight (1989) index of relatedness s (r) on the autosomal STR data, via their software program Kinship 1.1.2. The index was calculated with the following formula:

$$r = \frac{\sum \sum (P_y - P^*)}{\sum \sum (P_x - P^*)}$$

wherein P^* is the population frequency of each allele in the population, excluding the two individuals being compared, P_x and P_y are the frequencies of each allele in the compared individuals (*e.g.*, 0.5 if a heterozygote or 1.0 if a homozygote) and summations are over alleles and loci. If the samples are in Hardy-Weinberg equilibrium, the relatedness of parent-offspring dyads and sibling pairs should average 0.5. The theoretical range of the index is between -1.0 and 1.0 , with negative values indicating that two individuals share fewer alleles than expected by chance (Queller and Goodnight, 1989). We used overall allele frequencies from Woolley-Barker's (1999) trans-hybrid zone survey to calculate population frequencies of alleles. Other studies using microsatellites in variable populations indicate that relatedness estimates change little after 8–9 loci are sampled (Altmann *et al.*, 1996; Girman *et al.*, 1997).

RESULTS

Social Organization

Group H contained elements of both anubis and hamadryas social organizations. Overall, the group resembled a multimale, multifemale group that lacked cohesion. We observed frequent separation of foraging parties that regularly remained independent for several days. There were 4–7 hamadryas-like OMUs nested within an otherwise anubis-like group. At the beginning of observations there were three strict and one loose OMU, and by the end of the observation period there were three strict and four loose OMUs. Male and female members of OMUs are significantly more hamadryas-like in phenotype than non-OMU individuals (males: OMU mean PHI score = 8.14, $N = 7$; non-OMU mean PHI score = 12.04, $N = 14$; $F = 10.13$, $p < 0.01$; females: OMU mean PHI score = 9.68, $N = 14$; non-OMU mean PHI score = 12.75, $N = 12$; $F = 7.80$, $p = 0.01$).

In many cases, the OMUs in group H were as stable as those in pure hamadryas societies. In six of the eight OMUs, one or two females were in the OMU for the entire observation period of the OMU (13–39 mo). In the other two OMUs, there was a succession of different unit females ranging in tenure from 0.5 to 8 mo. Overall, OMU bonds with the same male ranged from 0.5 to >39 mos and, on average, movement of female into or out of an OMU occurred once every 2.4 mo. However, most of them moved between different OMUs and not out of an OMU altogether (Beehner and Bergman, *in press*). Only four females switched between OMU and non-OMU categories, and no male alternated between OMU and non-OMU categories. The emergence or disappearance of OMUs resulted only as OMU males immigrated ($N = 1$), disappeared ($N = 1$), or reached maturity ($N = 3$).

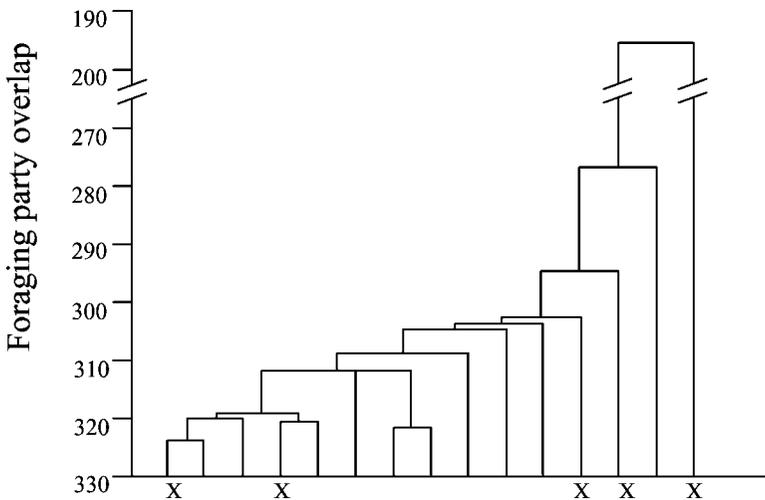


Fig. 1. Single-link cluster analysis tree of males in group H based on their tendency to occur in the same subgroup. Scores range from 0 (never together) to 500 (always together). X indicates males with one-male units.

However, other than the OMUs themselves, there was no evidence of a hamadryas-like, multilevel society. There was no organizational level between the OMU and the group as a whole, and foraging parties generally represented inconsistent associations of OMU and non-OMU individuals (Fig. 1). The lack of deep clusters in Fig. 1 indicates that, with the exception of one OMU male that frequently separated from the group (on the far right of the diagram), there was little consistency to foraging party formation. To help understand the scale of the diagram, the cluster of five males on the left of Fig. 1 were, on average, in foraging parties with each other only 3% more often than with the next most common foraging party partner. In contrast to our findings, Sugawara's (1979) cluster analysis on H (data from 1975) revealed that there were two distinct multimale subgroups, one of which contained two OMUs while the other contained four OMUs.

Foraging parties contained a greater percentage of group males during the dry season than during the wet season, indicating that dry season foraging parties were larger (dry season mean = 73%, $N = 150$; wet season mean = 57%, $N = 160$; $F = 20.50$, $p < 0.001$). This unexpected result (larger groups when food availability was lower) may be due to differences in predation risk across H's habitat. Although we do not have direct measures of predation risk, we qualitatively assessed predation risk according to foraging environment. Along the Awash River below the falls, there were two very distinct foraging environments for H: (1) inside the Awash canyon and

(2) outside the Awash canyon (grasslands). They differ qualitatively in visibility and refuge availability, two factors that are the major sources of variation in predation risk for baboons because they determine attack risk and capture risk (Cowlshaw, 1997a,b). Inside the 120 m Awash River canyon, H slept on cliffs and frequently foraged along the canyon's sloped walls and riverine forest. There, baboons were rarely more than 50 m from a refuge, i.e. a steep cliff or tall tree. During the dry season, there were few resources available inside the canyon; consequently, group members extended their day range outside the canyon to the surrounding grasslands where resources such as seeds of *Acacia nubica* and various roots were prevalent. H left the canyon to forage on the grasslands for 47% of days in the dry season versus 16% of days during the wet season. Outside the Awash canyon there are no cliffs and few trees to serve as refuges from predators. Refuge distance in the grasslands is typically greater than 100 m, and, because of the tall grass and lack of vertical structures, visibility is much lower on the grasslands than inside the canyon. Consequently, foraging outside the canyon carried a greater predation risk than foraging inside the canyon because both attack risk and capture risk were higher (Cowlshaw, 1997b). In support of this hypothesis, small groups occasionally were separated from the main group, yet only when foraging outside of the canyon did they appear nervous, give repeated contact calls, and search for the main group.

We compared the size of foraging parties on days when the baboons foraged inside the canyon with the days when they foraged outside the canyon, restricting the analysis to 283 days that we followed a single foraging party for most of the day. The foraging parties were larger, i.e. a greater percentage of males were in a single foraging party, when the group left the canyon than when they remained inside the canyon (inside canyon mean = 57%, $N = 189$; outside canyon mean = 84%, $N = 94$; $F = 56.01$, $p < 0.001$), both during the wet season (inside canyon mean = 54%, $N = 127$; outside canyon mean = 79%, $N = 25$; $F = 13.38$, $p < 0.001$) and the dry season (inside canyon mean = 62%, $N = 62$; outside canyon mean = 85%, $N = 69$; $F = 29.63$, $p < 0.001$).

Migration rates were very low in H. There was no evidence of female emigration or immigration, an observation consistent with both anubis and hamadryas groups (Abegglen, 1984; Pusey and Packer, 1987), though female movements between troops may occasionally occur in hamadryas societies (Sigg *et al.*, 1982). In contrast with a typical anubis group (Packer, 1979a), however, even male migration rates were low in H. During the 39-mo study, one male was killed by a hyena and one very old (>18 yrs.) and two middle-aged males disappeared. All males that disappeared appeared to be healthy on the last day of observation, and although we frequently encountered neighboring groups, we never saw them again.

The disappearances were most likely due to predation. However, even if we assume that the three disappearances were emigrations, the emigration rate was still considerably lower than for other groups in the Awash (Phillips-Conroy and Jolly, 2004). Six sub-adult males (almost certainly natal) reached maturity and consorted with adult females, and were still in the group at the end of the study. Furthermore, four males that were adults at the beginning of the study (1997) were previously trapped in the group as juveniles or subadults. Over the course of the study, only one male entered the group, a hamadryas-like hybrid (PHI score = 5.5).

To determine if there are genetic consequences to philopatry, we then evaluated how closely related group members were. In a trans-hybrid zone, microsatellite survey using genetic material from groups trapped in 1973 (including >75% of the baboons in the hybrid zone), Woolley-Barker (1999) found that average pairwise relatedness (r) was very low ($r = 0.01$ – 0.05) in the hybrid groups at the center of the hybrid zone (including group H), somewhat higher in the more anubis groups ($r = 0.09$ – 0.11), and very high in a pure hamadryas group ($r = 0.22$). She concluded that the high r in the hamadryas group reflected the rarity of migration, typical of hamadryas society. At the time (1973), H had a mean relatedness of 0.016. H's current mean relatedness has risen to 0.024. Separating the adults in H (mean $r = 0.010$) from the juveniles and infants (individuals born between 1997 and 2000; mean $r = 0.069$) indicates that r is higher in the younger members. Thus, the mean r for H appears to be increasing.

Table I is a summary of the composition of H through time. Group size increased considerably between the 1970s and 2000, but the mean PHI of the adult males in the group remained remarkably consistent. The percentage of males that had an intermediate PHI score (4.0–12.0), however, increased sharply between 1978 and 1997. The proportion of males and females in OMUs remained almost the same between Sugawara's study period and ours (Table I).

Table I. Group size and composition over time

Date	Group size	Adult males				Adult females	
		Total males	Mean PHI	OMU males	% Intermediate PHI ^a	Total females	OMU females
1975 ^b	63	13	11.1	6 (46%)	39%	20	13 (65%)
1978 ^b	69	14	10.1	5 (36%)	35%	19	9 (47%)
Sep. 1997	81	14	10.5	4 (29%)	78%	19	10 (53%)
Dec. 2000	96	17	10.6	7 (41%)	53%	26	13 (50%)

^aInterm. PHI (Phenotypic Hybrid Index) refers to males with $4 \leq \text{PHI} \leq 12$ for all years.

^bData from Sugawara (1979, 1982, 1988).

Mating System

Despite the presence of both anubis (promiscuous mating) and hamadryas (harem polygyny) mating systems in H, mating tended towards the hamadryas condition. During sexual consortships, H females rarely solicited copulations from extra-consort males, a behavior that occurs frequently in anubis baboons (Bercovitch, 1995; Ransom, 1981). Of 163 estrous cycles, a female only solicited copulation from an extra-consort male twice. Similarly, the male-male coalitions and consort harassments, frequently reported for anubis baboon troops (Noë, 1986; Packer, 1979b; Ransom, 1981; Smuts and Watanabe, 1990; Strum, 1982), were conspicuously absent from H. Instead, the hamadryas condition, where one male respects another male's possession of a female (Bachmann and Kummer, 1980; Kummer *et al.*, 1974), appeared to predominate. Male-male interactions on the whole were rare (each male-male dyad interacted only once every 53 h) and we could not determine a male dominance hierarchy.

In anubis groups, females typically mate with multiple males in each cycle and consort turnovers are common (Ransom, 1981; Smuts, 1985), while consort turnover is very rare in hamadryas society (Sigg *et al.*, 1982; Swedell, 2000). For H the percentage of consorts that involved a male turnover was 29%, a rate that is closer to the hamadryas condition. Furthermore, 74% of all consortships in H were between a male and a female with a prior history of association. Promiscuity was rare in OMUs as only 8 of 73 OMU female estrous cycles involved extra-unit copulations. On 12 occasions, two OMU females were in estrus simultaneously, and in 10 of them the OMU male was able to maintain exclusive access to both females.

Female promiscuity was more common across cycles. Over a representative 1-yr period, 8 of 16 females with multiple estrous cycles had multiple consort partners. Furthermore, of the females present for the entire study, all but one consorted with multiple males.

Social Structure

H contained elements of both anubis and hamadryas social structure with high variation in the strength of inter- and intrasexual bonds. Seven females had >66% of their grooming interactions with other adult females, while six females had >66% of their grooming interactions with adult males. The remaining 17 females had intermediate scores. The patterns broadly map onto OMU categories, with non-OMU females showing stronger bonds with females (interfemale grooming: non-OMU females: mean = 53%, range = 25–78%; loose OMU females: mean = 54%, range = 31–81%; strict OMU females: mean = 30%, range = 2–47%).

However, as the broad ranges in the OMU categories indicate, some females exhibited both interfemale and intersexual bonds, and some of the strongest grooming relationships in H were between female members of the same OMUs, particularly loose OMUs (Beehner, 2003).

Nearest neighbor data also mapped onto group substructure. The OMU leader male and unit females were in closer proximity with each other than with the rest of the group. The nearest neighbor to a strict OMU female was another member of her unit, 83.1% of the time, and 64.1% of the time the nearest neighbor was the leader male. Less than half the time (45.8%), a loose OMU female's nearest neighbor was another member of the unit, and in only 19.4% of observations was the nearest neighbor the leader male. Females outside of strict OMUs had consistent neighbors only 39.2% of the time (based on summed data on nearest male and nearest two females).

Although we distinguished loose OMUs from strict OMUs, we emphasize that, with one exception, all OMUs in the group deviated from the typical hamadryas pattern where males aggressively herd females and females follow males. In contrast, H OMU males followed females in their OMU more often than females followed males, and H OMU males rarely showed aggressive herding behavior towards unit females (Bergman, in press). Furthermore, all females in OMUs interacted with other group females, though this behavior occurs occasionally in hamadryas females (Colmenares, 1992; Kummer, 1984; Swedell, 2002).

Overall, the OMUs in H were less like typical hamadryas OMUs than reported by Sugawara. Sugawara (1979) found that OMU females typically followed the leader male and that leader males actively herded unit females. Sugawara (1988) did not describe an equivalent to the loose OMU, though in his 1978 observations, he noted that some of the OMUs appeared less cohesive than they had been in 1975.

In a comparison with published data from a pure anubis (Smuts, 1985), a pure hamadryas (Swedell, 2000), and a mostly-anubis Awash group that contained several immigrant hamadryas and hybrid males (Nystrom, 1992), we predicted that H would have intermediate levels of male-female bonding. We included data from the other Awash hybrid group (C) to analyze how the female composition of a group contributes to male-female bonding. Although C and H contained similar ranges of males, C females were all anubis. Thus, we predicted that H would fall between C and a pure hamadryas group in measures of male-female bonding. We report percentages of time from scan samples. Data from H males are from TJB's observations. Differences in published data preclude direct comparisons of the same behavioral measures across all groups; however, the results upheld our prediction. All males from H spent less time ≤ 0.1 m from a female

($N = 14$, mean = $20.6 \pm 6.7\%$, range 11–31) than males from the hamadryas group did ($N = 16$, mean = $59.1 \pm 9.3\%$, range 47–71; $F = 164$, $p < 0.001$). Ranges do not overlap, indicating that even the most cohesive OMU in H was not as spatially-cohesive as a pure hamadryas OMU. H males had a female within 10 m ($90.6 \pm 4.7\%$) more often than males from C did ($N = 12$, mean = $62.5 \pm 11.0\%$; $F = 75.6$, $p < 0.001$). Non-estrous H females had a male within 1 m (averaged for the 3 most common male neighbors, $N = 28$, $10.0 \pm 6.4\%$) more often than non-estrous females from a pure anubis group did (averaged for up to three male friends, $N = 32$, $1.0 \pm 1.3\%$; $F = 48.7$, $p < 0.001$). H males spent less time grooming females ($4.8 \pm 2.6\%$) than males from a pure hamadryas group did ($10.8 \pm 5.7\%$; $F = 12.9$, $p = 0.001$). H males had higher frequencies of grooming than males in C did (group C: $1.1 \pm 0.8\%$; group H: $4.8 \pm 2.6\%$; $F = 22.5$, $p < 0.001$) and H males had higher frequencies of being groomed than C males did (group C: $4.2 \pm 2.3\%$; group H: $12.3 \pm 3.1\%$; $F = 56.8$, $p < 0.001$). In sum, male-female proximity and grooming were more frequent in H than in C, but less frequent than in a pure hamadryas group.

For a more detailed comparison with C, we separated H males into three phenotypic categories to compare with the three phenotypic categories of Nystrom (1992). We divided the range of PHI scores into thirds to produce an anubis-like, an intermediate, and a hamadryas-like category. While not directly comparable to Nystrom’s phenotypic categories—the majority of H males would fall into C’s hybrid category—the separation allowed us to ask whether variation was greater within or between the two Awash groups. We compared across groups and categories for measures of proximity and grooming (Table II). For all measures, variation between categories within groups was less than the variation between groups: *female* ≤ 10 m, overall $F = 18.0$, $p < 0.001$, between categories $F = 2.2$, $p = 0.13$, between groups, $F = 71.1$, $p < 0.001$; *grooming female*, overall $F = 3.9$, $p = 0.12$, between categories $F = 0.01$, $p = 0.99$, between groups, $F = 15.3$,

Table II. Comparisons between different types of males in group H and group C for proximity and grooming Measures

Type of male	N	Female ≤ 10 m (% time \pm SD)	Grooming female (% time \pm SD)	Groomed by females (% time \pm SD)
Group C				
Hamadryas	3	71.5 \pm 8.7	1.5 \pm 0.7	7.7 \pm 0.7
Hybrid	4	61.6 \pm 9.8	0.7 \pm 0.3	3.1 \pm 1.2
Anubis	5	57.9 \pm 11.6	1.2 \pm 1.0	3.0 \pm 1.0
Group H				
Hamadryas-like	2	94.9 \pm 1.3	4.5 \pm 1.1	11.1 \pm 0.8
Intermediate	7	89.4 \pm 4.5	5.3 \pm 2.8	12.5 \pm 4.0
Anubis-like	5	91.0 \pm 5.6	4.2 \pm 3.2	12.6 \pm 1.4

$p = 0.001$; *groomed by females*, overall $F = 16.9$, $p < 0.001$, between categories $F = 1.2$, $p = 0.33$, between groups, $F = 54.6$, $p < 0.001$. Because intergroup variation was greater than within-group variation, it appears that the female composition of hybrid groups may be an important determinant of male-female bonding.

DISCUSSION

With the exception of emigration, H was intermediate between pure hamadryas and pure anubis in all aspects of its social system. The group contained one element of the hamadryas multileveled society, the OMU, in a group that was predominantly characterized by the multimale, multifemale organization of anubis societies. In addition, the hybrid group contained a novel social structure that was itself intermediate: the loose OMU. In general, the different elements of the social system coincided. Hamadryas-like OMUs contained both strong male-female social bonds and a harem polygynous mating system while individuals outside of OMUs were less focused on male-female bonds and exhibited more promiscuous mating. While the OMUs in the group showed long-term stability, the group lacked cohesion and, in some aspects, resembled a fission-fusion society.

Group H OMUs contained phenotypically more hamadryas-like individuals, which suggests that individual ancestry may determine many of the behaviors that affect social systems. However, the comparison between H and a mixed-male/anubis-female group indicated that group composition, in addition to individual ancestry, also plays a significant role in determining social structure. The interaction of individual ancestry, social setting, and social behavior for this group is explored in greater detail elsewhere (Bergman and Beehner, 2003).

Our qualitative analysis of H's substructure indicated that foraging party size was largely determined by predation risk in different habitats rather than by food availability across seasons. Our findings are supported by other observations in baboons. For example, Cowlshaw (1997b) showed that baboons under-utilize food-rich local habitats that have high predation risk. Kummer *et al.* (1985) reported that hamadryas OMUs do not coalesce to form the larger, multileveled society in the absence of predation. Anderson (1986) reported that subgroup formation is negatively correlated with predation risk across baboon populations.

Changes in Group H Between the 1970s and 1990s

In the absence of significant immigration, the size of H, consisting entirely of hybrids with an unusual and mixed social system, increased

substantially in three decades. For comparison, we looked at changes in the size of a group at the anubis end of the Awash hybrid zone that showed rapid growth during a previous behavioral study: group C (Nystrom, 1992). C increased from 80 individuals in 1988 (Nystrom, 1992) to 95 individuals in 2000 (pers. obs.), an average growth rate of 1.6% per year. H increased from 63 individuals in 1975 to 96 individuals in 2000, a higher average growth rate of 2.1% per year. The high reproductive output of hybrids contradicts the tension-zone model (Barton and Hewitt, 1985; Key, 1968), where the stability of a hybrid zone is maintained by a balance between migration and selection against hybrids. Instead, our results suggest that a bounded hybrid superiority model, where hybrids have greater success than parental individuals in a transitional environment (Moore, 1977), may be more appropriate.

Although initially very low, pairwise relatedness within H has increased since the 1970s and is continuing to rise. An increase in relatedness is almost certainly due to the rarity of emigration from the group. There are several possible explanations for the low rate of emigration. First, the hamadryas philopatric tendency (Abegglen, 1984; Kummer, 1968a; Sigg *et al.*, 1982) may predominate in a group with a high degree of hamadryas ancestry. Second, hybrids have unusual patterns of testicular development and may have a corresponding disruption in behavioral trajectories (Phillips-Conroy and Jolly, 2004). Third, hybrid males are smaller than anubis and hamadryas males (Phillips-Conroy and Jolly, 2004) and may be unwilling to enter other groups that contain larger males. Fourth, males may be choosing to stay in H because perceived mating opportunities (Alberts and Altmann, 1995) are higher in a hybridized natal group. Of the four explanations, the first appears least likely given the numerous occasions that hamadryas males have migrated into Awash groups (Phillips-Conroy *et al.*, 1992; Phillips-Conroy and Jolly, 2004). To evaluate the other three explanations, the factors that contribute to migratory decisions in different types of males needs further study.

H was more intermediate phenotypically and behaviorally than it had been during Sugawara's observations. That the changes occurred at the center of the Awash hybrid zone over a period of less than 25 years, suggests a dynamic hybrid zone. The dynamism indicates that the Awash hybrid zone may be fairly young because a stable equilibrium was not achieved by the 1970s. Other observations of major changes in the hybrid zone that occurred between 1968 and 1973 (Phillips-Conroy *et al.*, 1991, 1992; Phillips-Conroy and Jolly, 1986) support this hypothesis. A recent origin of the current hybridization between hamadryas and anubis baboons in the Awash does not preclude earlier episodes of hybridization.

ACKNOWLEDGMENTS

We thank our counterparts in Ethiopia for facilitating our work in the field: the Ethiopian Wildlife Conservation Organization (EWCO) and the Biology department of Addis Ababa University (AAU). In particular, at EWCO we want to thank the manager, Ato Tesefaye Hundesa, and the Wardens and staff of Awash National Park. At AAU we would especially like to thank the chairs of the biology department and our faculty associate, Dr. Solomon Yirga. We thank the co-directors of the Awash Baboon Project, Dr. Clifford Jolly and Dr. Jane Phillips-Conroy for their help both in the field and for helpful comments on an earlier version of this manuscript. We also thank Dawn Kitchen for her helpful comments on a previous version. This work was supported by Boise Fund, a Fulbright Student Grant, the National Geographic Society, the National Science Foundation, Sigma Xi, Washington University, and the Wenner-Gren Foundation.

REFERENCES

- Abegglen, J. J. (1984). *On Socialization in Hamadryas Baboons: A Field Study*, Associated University Presses, London.
- Alberts, S. C., and Altmann, J. (1995). Preparation and activation: determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol.* 36: 397–406.
- Aldrich-Blake, F. P. G., Dunn, T. K., Dunbar, R. I. M., and Headley, P. M. (1971). Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia Primatol.* 15: 1–35.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 229–267.
- Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C., and Bruford, M. W. (1996). Behavior predicts genetic structure in a wild primate group. *Proc. Natl. Acad. Sci.* 93: 5797–5801.
- Anderson, C. M. (1986). Predation and primate evolution. *Primates* 27: 15–39.
- Bachmann, C., and Kummer, C. (1980). Male assessment of female choice in hamadryas baboons. *Behav. Ecol. Sociobiol.* 6: 315–321.
- Barton, N. H., and Hewitt, G. M. (1985). Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* 16: 113–148.
- Beehner, J. (2003). Female Behavior and Reproductive Success in a Hybrid Baboon Group (*Papio hamadryas hamadryas* × *Papio hamadryas anubis*), PhD Thesis, Washington University, St. Louis, MO.
- Beehner, J. C., and Bergman, T. J. (in press). Social behavior among female hybrid baboons in the Awash National Park of Ethiopia. In Swedell, L., and Leigh, S. (eds.), *Reproductive strategies in baboons: Behavioral, ecological, and life history perspectives*, Kluwer Academic, Norwell, MA.
- Bercovitch, F. B. (1995). Female cooperation, consortship maintenance, and male mating success in savanna baboons. *Anim. Behav.* 50: 137–149.
- Bergman, T. J. (2000). *Mating Behavior and Reproductive Success of Hybrid Male Baboons (Papio hamadryas hamadryas × Papio hamadryas anubis)*, PhD Thesis, Washington University, St. Louis, MO.
- Bergman, T. J. (in press). Hybrid baboons and the origins of the hamadryas male mating strategy. In Swedell, L., and Leigh, S. (eds.), *Reproductive strategies in baboons: Behavioral, ecological, and life history perspectives*, Kluwer Academic, Norwell, MA.

- Bergman, T. J., and Beehner, J. C. (2003). Hybrid zones and sexual selection: Insights from the Awash baboon hybrid zone (*Papio hamadryas anubis* × *P. h. hamadryas*). In Jones, C. (ed.), *Sexual Selection and Primates: New Insights and Directions*, American Society of Primatologists, Norman, OK, pp. 500–537.
- Beyene, S. (1998). *The Role of Female Mating Behavior in Hybridization Between Anubis and Hamadryas Baboons in Awash, Ethiopia*, PhD Thesis, Washington University, St. Louis, MO.
- Brett, F., Turner, T., Jolly, C. J., and Cauble, R. (1982). Trapping baboons and vervet monkeys from wild, free-ranging populations. *J. Wildl. Manag.* 46: 164–174.
- Colmenares, F. (1992). Clans and harems in a colony of hamadryas and hybrid baboons: Male kinship, familiarity and the formation of brother-teams. *Behaviour* 121: 61–94.
- Cowlshaw, G. (1997a). Refuge use and predation risk in a desert baboon population. *Anim. Behav.* 54: 241–253.
- Cowlshaw, G. (1997b). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* 53: 667–686.
- DeVore, I., and Hall, K. R. L. (1965). Baboon ecology. In DeVore, I. (ed.), *Primate Behavior: Field Studies of Monkeys and Apes*, Holt, Rinehart, and Winston, New York, pp. 20–52.
- Dunbar, R. I. M. (1988). *Primate Social Systems*, Cornell University Press, New York.
- Dunbar, R. I. M. (1996). Determinants of group size in primates: A general model. *Proc. Br. Acad.* 88: 33–57.
- Dunbar, R. I. M., Hannah-Stewart, L., and Dunbar, P. (2002). Forage quality and the costs of lactation for female gelada baboons. *Anim. Behav.* 64: 801–805.
- Girman, D. J., Mills, M. G. L., Geffen, E., and Wayne, R. K. (1997). A molecular-genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). *Behav. Ecol. Sociobiol.* 40: 187–198.
- Kappeler, P. M., and van Schaik, C. P. (2002). Evolution of primate social systems. *Int. J. Primatol.* 23: 707–740.
- Key, K. (1968). The concept of stasipatric speciation. *Syst. Zool.* 17: 14–22.
- Kummer, H. (1968a). *Social Organization of Hamadryas Baboons: A Field Study*, University of Chicago Press, Chicago.
- Kummer, H. (1968b). Two variations in the social organization of baboons. In Jay, P. C. (ed.), *Primates: Studies in Adaptation and Variability*, Holt, Rinehart, and Winston, New York, pp. 293–312.
- Kummer, H. (1984). From laboratory to desert and back: A social system of hamadryas baboons. *Anim. Behav.* 32: 965–971.
- Kummer, H., Banaja, A. A., Abo-Khatwa, A. N., and Ghandour, A. M. (1985). Differences in the social behavior between Ethiopian and Arabian hamadryas baboons. *Folia Primatol.* 45: 1–8.
- Kummer, H., Götz, W., and Angst, W. (1974). Triadic differentiation: An inhibitory process protecting pair bonds in baboons. *Behaviour* 49: 62–87.
- Moore, J. (1978). Dominance relations among free-ranging female baboons in Gombe National Park, Tanzania. In Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology*, Academic, London, pp. 67–70.
- Moore, W. S. (1977). An evaluation of narrow hybrid zones in vertebrates. *Q. Rev. Biol.* 52: 263–278.
- Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol.* 19: 104–165.
- Newman, T. K. (1997). *Mitochondrial DNA Analysis of Intraspecific Hybridization in Papio hamadryas anubis, P. h. hamadryas and Their Hybrids in the Awash National Park, Ethiopia*, PhD Thesis, New York University, New York.
- Noë, R. (1986). Lasting alliances among adult male savannah baboons. In Else, J. G., and Lee, P. C. (eds.), *Primate Ontogeny, Cognition, and Social Behaviour*, Cambridge University Press, Cambridge, pp. 381–392.
- Nystrom PDA (1992). *Mating Success of Hamadryas, Anubis and Hybrid Male Baboons in a "Mixed" Social Group in the Awash National Park, Ethiopia*, PhD Thesis, Washington University, St. Louis, MO.

- Packer, C. (1979a). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* 27: 1–36.
- Packer, C. (1979b). Male dominance and reproductive activity in *Papio anubis*. *Anim. Behav.* 27: 37–45.
- Phillips-Conroy, J. E., and Jolly, C. J. (1986). Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. *Am. J. Phys. Anthropol.* 71: 337–350.
- Phillips-Conroy, J. E., and Jolly, C. J. (1988). Dental eruption schedules of wild and captive baboons. *Am. J. Primatol.* 15: 17–29.
- Phillips-Conroy, J. E., and Jolly, C. J. (2004). Male dispersal and philopatry in the Awash baboon hybrid zone. *Primate Rep.* 68: 27–52.
- Phillips-Conroy, J. E., Jolly, C. J., and Brett, F. L. (1991). Characteristics of hamadryas-like male baboons living in anubis baboon troops in the Awash hybrid zone, Ethiopia. *Am. J. Phys. Anthropol.* 86: 353–368.
- Phillips-Conroy, J. E., Jolly, C. J., Nystrom, P., and Hemmalin, H. A. (1992). Migrations of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. *Int. J. Primatol.* 13: 455–476.
- Pusey, A. E., and Packer, C. (1987). Dispersal and philopatry. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 250–266.
- Queller, D. C., and Goodnight, K. F. (1989). Estimating relatedness using genetic-markers. *Evolution* 43: 258–275.
- Ransom, T. W. (1981). *Beach Troop of the Gombe*, Bucknell University Press, London.
- Sigg, H., Stolba, A., Abegglen, J. J., and Dasser, V. (1982). Life history of hamadryas baboons: Physical development, infant mortality, reproductive parameters, and family relationships. *Primates* 23: 473–487.
- Smuts, B. B. (1985). *Sex and Friendship in Baboons*, Aldine, New York.
- Smuts, B. B., and Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male olive baboons (*Papio anubis*). *Int. J. Primatol.* 11: 147–172.
- Strum, S. C. (1982). Agonistic dominance in male baboons: An alternative view. *Int. J. Primatol.* 3: 175–202.
- Sugawara, K. (1979). Sociological study of a wild group of hybrid baboons between *Papio anubis* and *Papio hamadryas* in the Awash Valley, Ethiopia. *Primates* 20: 21–56.
- Sugawara, K. (1982). Sociological comparison between two wild groups of anubis-hamadryas hybrid baboons. *Afr. Study Monogr.* 2: 73–131.
- Sugawara, K. (1988). Ethological study of the social behavior of hybrid baboons between *Papio anubis* and *P. hamadryas* in free-ranging groups. *Primates* 29: 429–448.
- Swedell, L. (2000). *Social Behavior and Reproductive Strategies of Female Hamadryas Baboons, Papio hamadryas hamadryas, in Ethiopia*, PhD Thesis, Columbia University, New York.
- Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *Int. J. Primatol.* 23: 1205–1226.
- Woolley-Barker, T. (1999). *Social Organization and Genetic Structure in a Baboon Hybrid Zone*, PhD Thesis, New York University, New York.