RESEARCH ARTICLE

Behavioral Variation and Reproductive Success of Male Baboons (*Papio anubis* × *Papio hamadryas*) in a Hybrid Social Group

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We take advantage of an array of hybrid baboons (*Papio anubis* × *Papio hamadryas*) living in the same social group to explore the causes and consequences of different male mating strategies. Male hamadryas hold one-male units and exhibit a sustained, intense interest in adult females, regardless of the latter's reproductive state. Anubis baboons, by contrast, live in multi-male, multi-female groups where males compete for females only when the latter are estrous. These two taxa interbreed to form a hybrid zone in the Awash National Park, Ethiopia, where previous work has suggested that hybrid males have intermediate and ineffective behavior. Here, we first examine male mating strategies with respect to morphological and genetic measures of ancestry. We found significant relationships between behavioral measures and morphology; males with more hamadryas-like morphology had more hamadryas-like behavior. However, genetic ancestry was not related to behavior, and in both cases intermediates displayed a previously unreported level of behavioral variation. Furthermore, male behavior was unrelated to natal group. Second, we evaluated reproductive success by microsatellite-based paternity testing. The highest reproductive success was found for individuals exhibiting intermediate behaviors. Moreover, over nine years, some genetically and morphologically intermediate males had high reproductive success. We conclude that the behavior of hybrid males is therefore unlikely to be an absolute barrier to admixture in the region. Am. J. Primatol. 70:136–147, 2008.   © 2007 Wiley-Liss, Inc.

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INTRODUCTION

Despite a growing interest in primate sexual selection [e.g., Jones, 2003; Kappeler & van Schaik, 2004], comparatively little work has investigated reproductive strategies in primate hybrid zones. Hybrid zones are often considered ''natural laboratories'' for the exploration of the causes and consequences of behavioral variation [Hewitt, 1988]. Within a hybrid zone, animals with diverse genetic backgrounds can be examined in a common ecological and social context, allowing the proximate causes and fitness consequences of alternative behaviors to be discerned. This is particularly useful for behaviors relating to mating strategies whose expression might depend on the context of the social group.

Two closely related primates with very different mating strategies are hamadryas and anubis baboons (*Papio hamadryas* and *Papio anubis*). These taxa meet and hybridize in the Awash National Park, Ethiopia—home to at least ten social groups exhibiting signs of mixed ancestry to some degree [Nagel, 1973; Newman, 1997; Phillips-Conroy & Jolly, 1986;

Woolley-Barker, 1999]. The two parental species differ in both social organization and male mating strategies. Most significantly for the current study, among hamadryas, most mating occurs between members of harems (or one-male units, OMUs). Male hamadryas exhibit sustained, intense interest in adult females, regardless of the latter's reproductive state [Kummer, 1968a], and OMU males display constant vigilance and controlling behavior toward

their females. Establishing and maintaining these long-term bonds with females are critical for a hamadryas male's mating success [Kummer, 1968a]. Conversely, anubis baboons live in multi-male, multi-female groups, in which intense interactions between a male and his potential mates are limited to a female's receptive period [DeVore & Hall, 1965]. Male anubis are primarily interested in and compete for periovulatory females with which they form short-term consortships [Packer, 1979]. During such consortships, which last from a few hours to a few days, anubis males vigorously try to maintain close proximity with estrous females [Packer, 1979; Ransom, 1981]. At other times, males have few interactions with females, although they may form temporary nonsexual bonds with a female "friend" [Nystrom, 1992; Smuts, 1985]. Apart from such female friends, adult male anubis are generally intolerant of non-estrous females feeding near them. The differences between hamadryas and anubis mating strategies are thus most obvious during males' interactions with non-estrous females—rare and largely indifferent for anubis males versus frequent, attentive, and often tense for hamadryas males.

Several studies in the Awash hybrid zone have addressed both the causes and consequences of these differences in male behavior, capitalizing on the existence of "mixed" groups (i.e. groups including members of both parental taxa as well as hybrids) to examine the relationships between behavior, heritage, social context, and fitness [Beyene, 1993, 1998; Nystrom, 1992; Phillips-Conroy et al., 1991; Sugawara, 1979, 1982, 1988]. All found a positive relationship between ancestry and behavior: hybrids that looked more like hamadryas or anubis baboons, acted more like the parental species they resembled. This generally held true even for males living in the same group. Although suggestive of a genetic basis for the differences in male behavior, the history of the males in these studies was unknown, raising the possibility that these behavioral differences may result from differing social contexts in their natal troops.

Previous findings from the Awash further suggest that differences in male behavior have important fitness consequences that affect the dynamics of the hybrid zone. Hybridization occurs primarily through cross-migration of males (in both directions) and group fusion [Beyene, 1993; Phillips-Conroy et al., 1991, 1992; Sugawara, 1988]. It seems that a major determinant of genetic structure is the relative ability of males in the resultant mixed groups to compete for and acquire mates. Previous observations have suggested that phenotypically (i.e. morphologically) intermediate hybrid males father fewer offspring, not because of infertility but because they have intermediate and ineffective behavior [Nagel, 1973; Nystrom, 1992; Phillips-Conroy &

Jolly, 1981; Phillips-Conroy et al., 1991; Sugawara, 1979, 1988]. Low fitness of intermediate males would limit the potential for gene flow out of the hybrid zone. However, all the previous studies were based on broad comparisons of hybrid versus phenotypically "pure" males, and did not examine whether the relationship between phenotype and mating success also held true among hybrid males. Thus, it is unknown how selection might act within groups comprised entirely of hybrid males. Also unknown is the extent to which mating success in mixed and hybrid groups is reflected in production of offspring.

Here, we address these gaps in our knowledge using behavioral and genetic data from a group that occupies the same range as (and is probably descended from) a group previously studied by Sugawara [Sugawara, 1979, 1982, 1988]. In addition to a broad phenotypic spectrum, the group exhibits features of both hamadryas and anubis society with several OMUs embedded within a larger multi-male, multi-female group [Bergman & Beehner, 2004]. The objectives of this study were (1) to examine the determinants of male behavioral strategies, and (2) to determine the reproductive success of males with different ancestry and mating strategies.

First, we compare elements of each male's behavior toward non-estrous females as a function of his genotypically and morphologically expressed ancestry. In this group, males do not overtly compete for access to non-estrous females, and non-estrous females are always available. Thus, his interactions with non-estrous females provide a measure of a male's behavioral strategy that is minimally confounded by male–male competition and mating success. On the basis of previous studies, we predict a relationship between ancestry and behavior [Beyene, 1993, 1998; Nystrom, 1992; Phillips-Conroy et al., 1991; Sugawara, 1979, 1982, 1988]. Furthermore, several of the males are natal, having grown up in the group. On the basis of the hypothesis that experience determines mating behavior, we predict that the social milieu of a male's natal group will influence his behavior as an adult. Therefore, we also test the prediction that natal males (still living in the group as adults) will be behaviorally more alike than non-natal males.

Second, we compare behavior with offspring production, using microsatellite-based paternity testing of the 13 infants conceived during the time when behavioral observations took place, and an additional 50 offspring born in the group in the 7 years preceding and the 1 year following behavioral observation. On the basis of previous studies, we predict that males exhibiting "intermediate" behavior will have comparatively low reproductive success. Third, we compare ancestry to offspring production. We predict that intermediate scores on genotypic and phenotypic measures, indicating

significant admixture in an animal's ancestry, will be associated with low reproductive success.

We also address three other issues related to paternity. First, as there is considerable interest in the correspondence between observed mating behavior and paternity [Alberts et al., 2006], we compare observed mating success with genetically determined paternity. Second, we explore whether, as reported previously in male baboons, reproductive success peaks two to three years after reaching adulthood [Alberts et al., 2006]. Third, because hybrid males in the group are smaller in terms of body mass than either anubis or hamadryas males in the Awash population at large [Phillips-Conroy & Jolly, 2004], we examine body mass as a predictor of reproductive success.

METHODS

Study Group

The target group (Group H) is located at the phenotypic center of the Awash hybrid zone and its composition and relation to other groups has been described elsewhere [Bergman, 2000; Beyene, 1998; Kummer, 1968b; Nagel, 1973; Newman, 1997; Nystrom, 1992; Phillips-Conroy & Jolly, 1986; Woolley-Barker, 1999]. During behavioral observation (1997–1998), Group H comprised 80–84 individuals, including 15 adult males and 26 adult females. The social structure of the group exhibits elements of both hamadryas and anubis society, with some males forming OMUs (29%). In the 20 years between Sugawara's [1979, 1982, 1988] and this study, males in Group H have become more intermediate in morphology and behavior [Bergman & Beehner, 2004], and a novel, intermediate type of social organization has appeared [i.e. less spatially cohesive or ''loose OMUs'', Beehner & Bergman, 2006]. More details on the social structure of the group and the methods of classifying ''loose'' and ''conventional'' OMUs can be found elsewhere [Beehner & Bergman, 2006; Bergman & Beehner, 2004]. We were unable to detect a male dominance hierarchy of the kind seen in anubis baboons.

Data Sets

The 15 males observed during behavioral observations (''current males'') are a subset of our larger data set used in paternity analysis (Table I).

TABLE I. Summary of Potential Fathers in Group H

Name or ID	Birth year	Natal male[a]	OMU[b] size	OMU type	Factor 1 score	Mating success[b]	Current reproductive success[b]	Total reproductive success[b]	PHIS	GHIS	Body mass (kg)
91001	1973							−2.39	9.0	−0.65	22.7
91003	1973							−2.69	11.0	−0.22	20.0
91009	1979							0.21	10.0	0.43	22.7
95030	1981							3.31	6.0	−0.70	20.9
95051	1981							−0.49	14.0	0.55	20.0
91005	1982							−1.59	14.0	0.06	22.7
91012	1982							0.81	9.0	−0.55	21.4
91008	1984							−0.69	14.0	−0.22	20.5
95028	1985							1.41	10.0	−0.12	20.9
95045[b]	1988							−0.09		−0.01	
LR	1980	—	—	None	−0.74	0.0	0.0	−1.59	10.0	0.43	18.2
MP	1980	—	1	Strict	1.79	0.0	0.0	−1.49	5.0	−0.46	16.4
HO	1982	—	—	None	−0.74	0.5	0.0	−1.99	10.0	−0.39	16.4
ME	1982	—	—	None	−1.12	0.0	0.0	−2.79	14.0	0.55	16.4
FX	1983	—	1	Strict	0.73	0.0	0.0	0.51	6.0	−0.87	20.5
MA	1983	—	—	None	−0.01	1.0	1.0	4.71	13.0	0.25	20.5
BZ	1985	—	—	None	−0.87	0.0	0.0	−1.59	10.5	−0.43	17.3
AN	1986	—	—	None	0.19	3.0	3.0	2.51	8.5	−0.38	14.5
CA	1986	Yes	4–6	Strict	2.21	4.0	3.0	1.11	10.0	0.72	19.5
GR	1987	—	—	None	−0.80	0.0	0.0	−0.29	10.5	0.31	17.3
LI	1987	Yes	—	None	−0.80	1.0	1.0	1.11	12.0	−0.34	20.0
HT	1988	—	—	None	−0.48	0.0	0.0	−0.69	12.0	−0.21	18.2
CD	1989	Yes	—	None	−0.19	1.0	1.0	0.31	14.0	−0.15	16.4
GO	1989	Yes	4	Loose	0.82	2.5	4.0	2.71	9.0	0.10	19.1
BU	1991	Yes	1	Loose	0.13	0.0	0.0	−0.39	14.0	−0.27	16.8

[a]Natal males were trapped in the group as juveniles or had a father that lived in the group.
[b]OMU, one-male unit. Mating success, number of consorts that resulted in pregnancy; Current reproductive success, number of offspring during behavioral study; Total reproductive success, residuals from regression of total number of offspring on reproductive tenure.
[c]Only observed as a subadult—not all data are available.

For the 15 current males we have data on behavior, appearance, body mass, age, genetics, mating success, and paternity success during the observation period ("current reproductive success", Table I). There are an additional ten adult males that had previously been observed in the group, for whom we have all but behavioral data and mating success data. These comprise the "total" data set of 25 potential fathers. In addition, the total data set includes paternity information for all 63 sampled animals born in the group between 1990 and 1999, which is used to calculate "total reproductive success" for all males (Table I). Although the larger "total" data set lack behavioral data, it greatly increases the sampling window and the number of offspring for our analyses of reproductive success.

Observational Data

Group H was observed between August 1997 and November 1998. Focal animal observation proved unfeasible in the dense thornscrub and difficult terrain of the gorge where Group H spent most of its time. Therefore, data were collected primarily through all-occurrence and scan sampling [Altmann, 1974], which permitted data to be collected throughout the group's range, rather than at an artificial provisioning site [the method previously used for this group; Sugawara, 1979, 1988].

All observed occurrences of *grooming*, *herding*, *leading*, and *following* were recorded. *Herding* included female-directed neck-biting, dragging, pushing, eye-lid threats, and yawning in attempts to move females [Bergman, 2000]. *Leading* and *following* were scored when one individual moved and another followed <5 m behind. During observations, a scan sample [Altmann, 1974] was collected every 5 min, recording each adult in view and the estimated distance to their nearest female neighbors. We standardized the all-occurrence data by dividing the number of times a male executed the behavior of interest by the observation time for that male (the total number of scans for that male multiplied by 5 min). Observations collected while the male was consorting with an estrous female were excluded from this calculation.

Because female baboons, like many primates, exhibit obvious perineal swellings during the follicular and ovulatory phases of their reproductive cycle [e.g., Gesquiere et al., 2006], we could easily distinguish estrous from non-estrous females. Each day, we scored the reproductive condition of females as "estrous" (having any degree of perineal swelling) or "non-estrous" (having flat perineal skin, including pregnant and lactating females). Each day we also scored an adult male as "unpaired" (if he had no particular female as his nearest neighbor more than 50% of the day [Bergman, 2000]) or "paired" (if a female was his nearest female neighbor for 50% or more of observation time). In practice, for males with multiple females in their OMU, unit females accounted for more than 80% of female neighbors. Males paired with estrous females were classified as *in consort* (and the relationship between a male and an estrous female is hereafter referred to as a *consortship*); all others were classified as *non-consort*.

In unhybridized populations, hamadryas males are attentive to females regardless of reproductive state [Kummer, 1968a], whereas anubis males exhibit relatively low levels of association with non-estrous females [Nystrom, 1992; Smuts, 1985]. To express variation in this feature among hybrid males, we devised an index of their interest in non-estrous females that included six variables. A male's *association with females* was the number of days he spent paired with a non-estrous female minus the number of days he spent unpaired. This variable indicates each male's hamadryas-like propensity to associate with non-estrous females, unbiased by the amount of time he spends in consort [Bergman, 2000]. The remaining variables were also all derived from non-consort data: *distance to nearest female* was the average distance between a male and his nearest female neighbor; *grooming*, *herding*, *leading*, and *following* were each male's rate of these behaviors, as directed toward females.

For comparison to results from paternity testing ("reproductive success", described below), we scored "mating success" based on consortships that resulted in an infant for which genetic data were available. If more than one male consorted with a female during the periovulatory period of her conceptive cycle [i.e. the five days preceding deturgescence of perineal skin; see also Gesquiere et al., 2006], mating success was allotted to the males in proportion to the number of days each male spent in consort. These values were summed to provide a measure of each male's mating success.

Trapping and Sampling

Animals from the group were trapped in 1991, 1995, 1998, and 2000. In 1991, 1995, and 1998, all adult males in the group were sampled. In 1995 and 1998, the majority of the group (including juveniles) was sampled. In 2000, all previously untrapped mothers (except 1) and all living infants conceived during the behavioral study were sampled. Animals were trapped in steel cages baited with corn using remotely triggered doors [Brett et al., 1982]. Once captured, animals were immobilized using ketamine, the dentition was examined, and body mass was determined by suspending the animal from a spring balance. In all seasons except 2000, blood was taken (from the femoral vein); in 2000, hair follicles were collected instead of blood. The blood was centrifuged, the "buffy coat" was removed, and samples were

immediately frozen. Tissue was also collected from two infants that died during behavioral observations. DNA was purified with Qiagen extraction kits (Qiagen Inc. Velancia, CA). All animal handling procedures were approved by the Institutional Animal Care and Use Committee of Washington University and/or New York University, and all research was conducted with approval of the Ethiopian Wildlife Conservation Organization.

Genetic Analysis

Animals were analyzed at 11, unlinked, microsatellite loci (ten autosomal and one Y-chromosomal loci). Microsatellite loci were amplified with human MapPair primers D2S1399, D3S1766, D4S243, D5S457, D6S1280, D7S817, D11S2002, D12S375, D142306, D19S716, and DYS391 (Research Genetics, Inc.). DNA was polymerase chain reaction-amplified using fluorescent-labeled primers with PerkinElmer Thermocycler 2400 or 9600s (PerkinElmer Life and Analytical Sciences, Inc. Waltham, MA) in a ''touch-down'' program under ''hot start'' reaction conditions using heat-activated *AmpliTaq* Gold polymerase [Woolley-Barker, 1999]. Samples were electrophoresed using ABI 377 and 310 automatic sequencers using 4.0% denaturing gels or polymers and visualized with GeneScan software (Applied Biosystems, Inc. Foster City, CA). A size standard (TAMRA 500) was included in each lane and alleles were scored manually. All loci were analyzed at least twice and homozygotes were analyzed at least three times. If discrepancies were found, samples were rerun until the same result was achieved three times consecutively or, failing that, were left unscored (5.0% of alleles).

Measures of Ancestry

Two different measures of ancestry were assessed, which by convention [Nagel, 1973] are called ''hybrid indices'', although they are scaled to the typical anubis condition rather than to hybridity per se. The phenotypic hybrid index (PHI) is based on morphological character states used previously to classify Awash baboons [Nagel, 1973; Phillips-Conroy & Jolly, 1986], with the addition of extra intermediate states expressing finer degrees of morphological intermediacy in hybrids [Bergman & Beehner, 2003]. Eight morphological characters were scored: mane color, mane length, face color, cheek tuft color, cheek tuft shape, tail shape, anal patch shape, and anal patch skin color. For each character, a score of 0.0 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. Scores were summed across characters, yielding a range from 0.0 for a pure hamadryas phenotype to 16.0 for a pure anubis. PHI scores for Group H males ranged from 5.0 to 14.0. To be consistent with previous publications, we use the term phenotypic hybrid index, although ''phenotype'' in this index refers solely to morphology and not behavior. Although the genetic basis of these character states is unknown, the PHI is thought to provide a good measure of individual ancestry [Nagel, 1973; Phillips-Conroy & Jolly, 1986]. The characters have been observed to sort independently [Nagel, 1973], are evenly weighted, and their extreme states are completely diagnostic. Individuals produced by crosses of apparently pure parents have PHI scores close to 8.0, as expected for animals with equal hamadryas and anubis ancestry.

The genetic hybrid index (GHI) used here is based on the index designed by Woolley-Barker [1999] and uses ten microsatellite loci (one Y-chromosomal and nine autosomal loci, D5S457 was not used in the hybrid index). In the Awash baboons, these markers are not completely taxon-diagnostic, but they exhibit taxon-distinctive allele frequencies in samples consisting of individuals with little obvious admixture [Woolley-Barker, 1999]. Such ''semi-diagnostic'' markers, when used in combination, effectively permit the accurate diagnosis of overall individual hybrid ancestry, even after generations of hybridization [Bert & Arnold, 1995].

On the basis of the allele frequencies in samples of phenotypically ''pure'' anubis and hamadryas baboons, each allele was given an ''allele diagnosticity value'', which equals the frequency of the allele in the pure anubis individuals minus the frequency of the allele in the pure hamadryas individuals [Woolley-Barker, 1999]. Allele diagnosticity values were summed across loci to create a GHI score for each animal, and these values were standardized against Woolley-Barker's [1999] larger sample, so that -1.0 represents the most hamadryas-associated and 1.0 the most anubis-associated genotype. GHI scores of Group H males ranged from -0.87 to 0.72.

All males were separated into categories based on PHI and GHI scores. We categorized ancestry by dividing the PHI and GHI ranges seen in Group H males into thirds: hamadryas-like (PHI = 5.0 to 8.0, $N = 3$; GHI = -0.87 to -0.34, $N = 9$), intermediate (PHI = 8.5 to 11.0, $N = 12$; GHI = -0.33 to 0.24, $N = 9$), and anubis-like (PHI = 11.5 to 14.0, $N = 9$; GHI = 0.25 to 0.72, $N = 7$). The same male could be classified in different PHI and GHI categories.

Assigning Paternity

We attempted to assign paternity to all 63 sampled animals born from January 1990 until December 1999. Males were considered as potential fathers if they were (1) known to have been resident in the group at the time, and (2) old enough (see below) to be the parent of the individual being tested. Additionally, two males from a neighboring group were included as negative controls. In all cases in

which paternity was assigned, the control males could be excluded. Maternal information was used to aid in paternity assignment of young infants with a known mother (22 cases). Paternity was assigned to all other individuals by using only the genotypes of the potential offspring and fathers. Paternity was tested by exclusion, performed manually, and analyzed by likelihood methods using Cervus 2.0 [Marshall et al., 1998]. Paternity was assigned by exclusion when all males but one were excluded by their genotype at two or more loci (46 cases). For the analysis using Cervus, we set the error rate at 1.0% (calculated from 22 known mother–infant pairs) and for the paternity simulation we used the following values: 15 candidate males (the most ever observed in the group), 95% of males sampled, 95% of loci typed, and 10,000 simulation cycles. Cervus resulted in 46 cases in which paternity was assigned with 95% likelihood. In 37 cases, results from exclusion and Cervus matched exactly, whereas in other cases results from exclusion and Cervus only differed in certainty, not in identity of the father. In nine cases, exclusion resulted in a single father while Cervus assigned paternity to that father at the 80% level. In seven cases, Cervus assigned a father at the 95% level, whereas exclusion identified two or three possible fathers, one of which was always the father assigned by Cervus. In two cases, Cervus assigned at the 95% level a father that had been excluded by one locus, whereas all other potential fathers were excluded by at least three loci. Therefore, paternity was assigned either if (1) Cervus assigned paternity at the 95% level, or (2) exclusion resulted in a single father. In total, 55/63 individuals were assigned paternity, including all 13 infants conceived during the period when behavioral observations took place. Using results only from exclusion or only from Cervus at the 95% level did not significantly alter our results.

We used paternity data to measure "reproductive success" in two ways. First, we calculated *current reproductive success* for each current male by determining the number of offspring each male sired during the behavioral study period. All potential fathers ($N = 15$) resided in the group throughout this period, and all offspring conceived during this time ($N = 13$) were assigned to fathers. Second, we calculated *total reproductive success* for each male by determining the total number of offspring sired by each male, based on all 55 cases of assigned paternity, controlled for the length of a male's residence as an adult in the group (i.e. his reproductive tenure). To calculate reproductive tenure, we set the age of male reproductive maturity at six years—a conservative estimate [Alberts & Altmann, 1995]. Information from age estimation (see below) and previous trappings allowed us to calculate each male's maximum and minimum possible reproductive tenure; the average of the two was used as the

best estimate. As expected, reproductive tenure was significantly correlated with the number of fathered offspring ($r^2 = 0.55$, $P = 0.005$). We therefore regressed the number of offspring on tenure duration, and used the unstandardized residuals of this regression as our measure of *total reproductive success*. In this measure, positive values indicate males with relatively high reproductive output for their reproductive tenure (Table I).

Natality, Age, and Weight

To address the effects of early social experience on adult behavior, we separated natal males from other males. "Natal males" ($N = 5$) were males observed in the group as juveniles and males whose father lived in the group [as determined by paternity testing; Bergman, 2000]. Males that did not meet these criteria were grouped together as "non-natal males" ($N = 10$), although it is possible that some of these were natal males that escaped detection.

Dental wear [Phillips-Conroy et al., 2000] or eruption status [for males trapped as juveniles; Phillips-Conroy & Jolly, 1988] was used to estimate ages of all animals trapped. To look for changes over time, we divided the total male dataset ($N = 25$) in half by age, which resulted in a group of 13 males with estimated birth dates between 1973 and 1983 (hereafter, *prior males*) and a group of 12 males with estimated birth dates between 1984 and 1991 (hereafter, *recent males*). All potential fathers trapped as adults ($N = 24$) were weighed. For males trapped multiple times, mean body mass was used.

Data Analysis

Because none of our datasets deviated significantly from normal (at $P = 0.05$) by the Kolmogorov–Smirnov test (SPSS v.10 for Macintosh), parametric statistics were used for all analyses. Pearson correlation was used to test for relationships between variables. For reproductive success analyses, both linear and quadratic regressions were used to identify curvilinear relationships in which the mid-range of the variable was associated with low (or high) success. In cases where regression analyses were not significant, analysis of variance (ANOVA) was used to examine categorical comparisons. All tests were two-tailed, and the significance level was set at $P = 0.05$.

RESULTS

Ancestry Measures

GHI was not significantly correlated with the PHI for the 15 current males living in the group in 1997–1998 ($r = 0.41$, $P = 0.13$). However, in the total sample of 25 males used in the study of genetic paternity, the GHI and PHI were significantly correlated ($r = 0.49$, $P = 0.02$). Although the larger

sample size might explain the discrepancy, it is also possible that the strength of the relationship between PHI and GHI may have changed over time. We therefore examined the relationship between PHI and GHI in *prior* (born before 1984) and *recent males* (born after 1984, see Methods), respectively. Among *recent males* there was no correlation between PHI and GHI ($r = -0.28$, $P = 0.40$), whereas among the *prior males* the relationship was significant, and much stronger than in the combined sample ($r = 0.77$, $P = 0.002$).

Behavior and Ancestry

The six behavioral measures designed to describe interest in nonreproductive females were subjected to principal components analysis. This yielded two factors with eigenvalues > 1.0. Table II shows the loadings of the behaviors on Factors 1 and 2. Males with high scores on Factor 1, accounting for 48% of the variation in the data, (1) frequently associated with non-estrous females, (2) had low average non-consort distance to females, and (3) led, herded, followed, and groomed non-estrous females at high rates. In sum, Factor 1 reflects a male's ''hamadryas-ness'' or ''anubis-ness'' with respect to his interaction with females. Factor 2 did not consistently separate anubis and hamadryas behavioral tendencies and thus will not be considered further.

Males with more hamadryas appearance (i.e. lower PHI) had more hamadryas-like (i.e. higher) scores on Factor 1 (Fig. 1A, $r = -0.55$, $P = 0.03$). However, phenotypic intermediates were found at both extremes of Factor 1. For example, males with the highest and second lowest scores on Factor 1 had PHI scores of 10.0 and 10.5, respectively.

In contrast, no relationship was found between Factor 1 and GHI (Fig. 1B; $r = -0.001$, $P = 0.99$). This was largely because of one male who was genetically the most anubis-like but behaviorally the most hamadryas-like (phenotypically, he was intermediate). After this male was removed from the analysis, there was a weak nonsignificant trend for

hamadryas-like Factor 1 scores to correlate with more hamadryas-like GHI ($r = -0.44$, $P = 0.12$). The behavioral variation found among natal males was considerable (Fig. 1A and B), and the variance in Factor 1 was actually higher among natal males (1.32) than it was among other males (0.81).

Mating and Reproductive Success

Mating success was significantly correlated with short-term reproductive success ($r = 0.93$, $P < 0.001$). Paternity was predicted accurately by the consortships recorded during behavioral observations, with three exceptions. In one case, behavioral and genetic measures assigned paternity to different males; in another case, paternity testing assigned paternity to one of two males that had consorted with the mother in the conceptive cycle; and in a third case, exclusion assigned paternity to two males, one of which was assigned paternity by Cervus and was also the only male that had been observed to consort with the mother in the conceptive cycle.
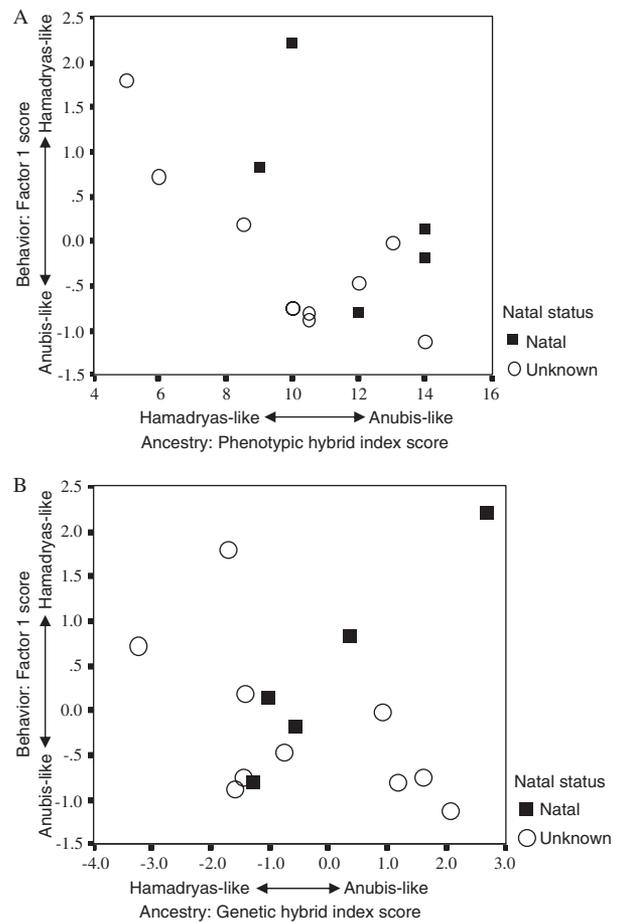
Fig. 1. Relationship between male phenotypic hybrid index scores (**A**), genetic hybrid index scores (**B**) and Factor 1 scores (a behavioral measure of ''hamadryas-ness''), separated by natal status.

TABLE II. Loading Scores on Factors 1 and 2 for Factor Analysis Using Six Behavioral Measures

Behavior	Factor 1	Factor 2
Association with females[a]	0.827	−0.126
Distance to females[b]	−0.596	0.645
Following females[c]	0.611	−0.516
Leading females[c]	0.752	0.609
Herding females[c]	0.801	0.504
Grooming females[c]	0.500	−0.115

[a]Difference between days alone and days associated with a non-estrous female.
[b]Average non-consort distance to a female.
[c]Rate of non-consort behavior directed toward females.

Behavior and Reproductive Success

First, while no linear relationship emerged between Factor 1 and *current reproductive success*, there was a nonsignificant trend for males with more hamadryas-like behavior to have higher success ($r^2 = 0.24$, $P = 0.06$). Second, although quadratic regression was not significant ($r^2 = 0.27$, $P = 0.15$), the shape of the curve describing the relationship was opposite to our prediction—rather than lower success, males with intermediate behaviors had the highest success (Fig. 2A). For the total data set, quadratic ($r^2 = 0.40$, $P = 0.047$) but not linear regression ($r^2 = 0.11$, $P = 0.23$), revealed a significant relationship between Factor 1 and *total reproductive success*, indicating that behaviorally intermediate males were associated with the highest success (Fig. 2B).

Ancestry and Reproductive Success

Among the 15 current males, there was no relationship between PHI and *current reproductive*

Fig. 2. Relationship between Factor 1 scores (a behavioral measure of "hamadryas-ness") and current offspring (the number of offspring fathered during behavioral observations; **A**) or offspring residuals (a measure of reproductive output controlling for reproductive tenure; **B**).

success (linear: $r^2 = 0.02$, $P = 0.64$; quadratic: $r^2 = 0.15$, $P = 0.38$) or between GHI and *current reproductive success* (linear: $r^2 = 0.07$, $P = 0.36$; quadratic: $r^2 = 0.07$, $P = 0.66$). Furthermore, we found no evidence of lower *current reproductive success* among intermediate males as there were no differences across categories (ANOVA, GHI: $F_{2,12} = 0.21$, $P = 0.82$; PHI: $F_{2,12} = 1.28$, $P = 0.31$). In fact, the following observations contradict our prediction: (1) although not significant, phenotypically and genetically intermediate males had a higher mean number of offspring than more "pure" males, (2) the male with the most offspring was both phenotypically and genetically intermediate, and (3) all three males that fathered multiple offspring were phenotypic intermediates.

Total reproductive success was unrelated either to PHI (linear: $r^2 = 0.04$, $P = 0.36$; quadratic: $r^2 = 0.04$, $P = 0.65$) or to GHI (linear: $r^2 < 0.001$, $P = 0.92$; quadratic: $r^2 = 0.001$, $P = 0.99$). Additionally, no differences were found among ancestry categories (ANOVA, PHI: $F_{2,21} = 0.26$, $P = 0.78$; GHI: $F_{2,22} = 0.06$, $P = 0.94$), although in both cases intermediate males had the lowest mean. This pattern was opposite to the results for *current reproductive success*, suggesting that the reproductive success of intermediate hybrids may have increased over time. Therefore, we subsequently examined the *total reproductive success* for intermediate males only, separating *prior* from *recent males*. For both genetic and phenotypic intermediates, *recent males* had higher reproductive success (PHI: $F_{1,10} = 6.29$, $P = 0.03$, GHI $F_{1,7} = 6.7$, $P = 0.04$) than *prior males*. Although this difference might result from more complete sampling of recent offspring, this seems unlikely because, among all males (males of all phenotypic and genetic categories), *recent males* have no advantage over *prior males* ($F_{1,23} = 1.31$, $P = 0.26$). Thus, it appears that the relative success of intermediate males has increased over time.
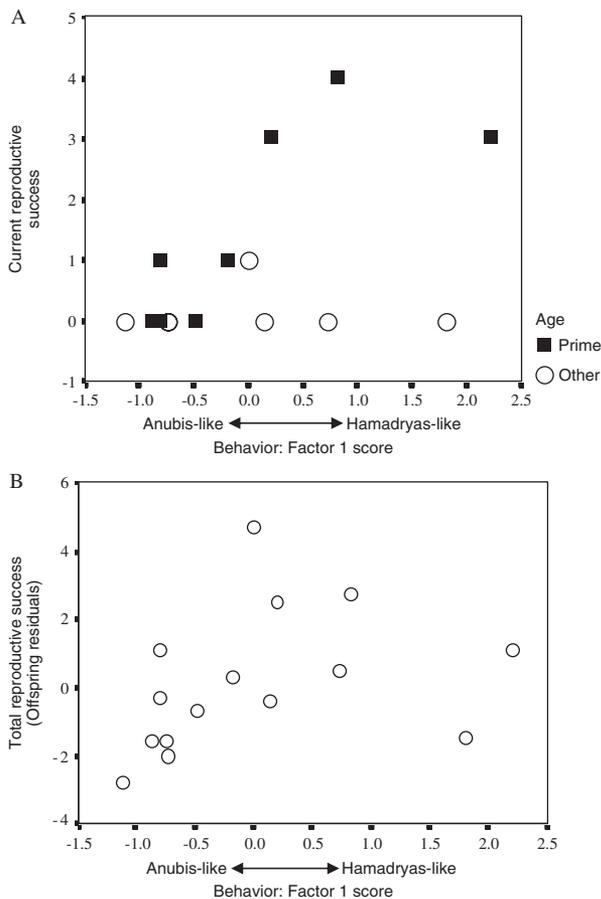
Age, Weight, and Success

For the total data set, we analyzed the distribution of ages based on the father's age at the time of each offspring's birth. Males aged 8–14 years old fathered the majority of offspring, whereas younger and older males produced relatively few offspring (Fig. 3). Males 8–14 years old ("prime-age males") fathered 85% of the offspring, significantly more than expected from the proportion of prime-age potential fathers (binomial $P < 0.001$). Because total reproductive success represents reproductive output over several years (0.5–8.0 years, mean 4.0 years), for all but two males, data are included from the "prime-age" years. Thus, age is unlikely to be confounding relationships involving total reproductive success. Among current males, prime-age males (age 8–14
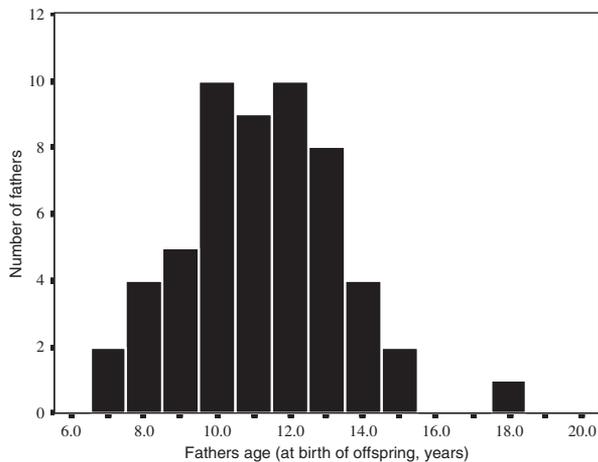
Fig. 3. Histogram of the ages of the fathers for each of 55 offspring.

years, $N = 8$) also had significantly higher *current reproductive success* than other males (prime males: 1.5 offspring; other males: 0.14 offspring; ANOVA: $F_{1,13} = 4.74$, $P = 0.048$). However, prime-age males did not differ from other males in behavior (Factor 1, ANOVA: $F_{1,13} = 0.0$, $P = 1.0$, Fig. 2A) or ancestry (PHI, ANOVA: $F_{1,13} = 0.13$, $P = 0.73$; GHI, ANOVA: $F_{1,13} = 0.07$, $P = 0.80$). Thus, age is unlikely to be confounding other results. Body mass was not related to *current* or *total reproductive success* (current: $r = 0.11$, $P = 0.69$, $N = 15$; total: $r = 0.12$, $P = 0.57$, $N = 24$).

DISCUSSION

In this study, ancestry (as measured by morphology but not by genetics) was a significant predictor of male behavior, even though the sample comprised only hybrid males. Males with more hamadryas-like appearance had more hamadryas-like behavior. Furthermore, natal males exhibited extremely variable behavior, suggesting that the social environment in which a male matures does not significantly influence his adult behavior. Taken together, these results suggest a genetic basis for some of the behavioral differences observed here, in agreement with a growing body of evidence indicating that even subtle behavioral variation in primates may have genetic bases [e.g., Erhart et al., 2005; Maestripieri, 2003; Trefilov et al., 2000]. In contrast, the lack of a relationship between GHI and behavior argues against such an interpretation and the issue warrants further exploration. It may be the case that the genes measured in the PHI are more directly linked to behavior (either through linkage or pleiotropy), or that the PHI is better at ''capturing'' a male's ancestry, perhaps owing to the more diagnostic nature of the characters involved.

Contrary to previous reports [Nystrom, 1992; Sugawara, 1988], ancestry and behavior were only weakly correlated and intermediates exhibited high variation in behavior (Fig. 1). The weak relationships might be caused by the hybrid nature of all males in this study. Indeed an intergroup comparison of male–female bonding supports this view as all Group H males were intermediate between ''pure'' anubis and hamadryas males [Bergman & Beehner, 2004].

The strong relationship between behavioral paternity (predicted from observations of behavior) and genetic paternity (determined from genotyping) supports the use of behavioral estimates for paternity when genetic data are not available. This coincides with findings from yellow baboons in Amboseli, Kenya [Alberts et al., 2006; Altmann et al., 1996; Buchan et al., 2003].

Contrary to predictions, where differences were found, intermediate male behavior was associated with the highest reproductive success. Furthermore, neither phenotypic nor genetic ancestry measures were related to a male's reproductive success. Thus, we found no evidence of hybrid disadvantage. Indeed, among the current males, the differences (although not significant) were in the opposite direction, suggesting that a failure to find a hybrid disadvantage was not merely the result of small sample size. Among Group H males, offspring production peaked shortly after reaching adulthood (Fig. 3), as also found among baboons elsewhere [Alberts et al., 2006]. Body mass was unrelated to reproductive output, indicating that the low body mass of hybrid males does not limit their success, at least not in the context of Group H. In sum, unlike previous studies in the Awash hybrid zone, our results indicate that behaviorally and phenotypically intermediate males can have high reproductive success. The difference, we believe, is real (and not due to the fact that previous studies used behavioral rather than genetic indicators of paternity) because the two measures are highly correlated. Indeed, our behaviorally and phenotypically intermediate males also had high mating success (data not shown). The success of males with intermediate behavior and ancestry at the time of our study may relate to the fact that by this time, Group H included a majority of animals of intermediate heritage, and exhibited a social structure with features intermediate between those of the parental species. Like hamadryas males, many of the group's adult males had remained in their natal group beyond the age at which almost all anubis males disperse. Moreover, similar to a hamadryas group (or ''band''), Group H frequently split into temporary subgroups that often remain separate for several days [Bergman & Beehner, 2003]. These were, however, inconsistent in membership, unlike the conventional OMU foraging subgroups of hamadryas.

Much of this social intermediacy, as well as the reproductive success of intermediate males, may be attributed to the fact that Group H females at the

time of the study were also recognizable hybrids, whose behavior varied in accordance with their ancestry. In particular, they varied in the extent to which they formed lasting bonds with a single male at the expense of bonds with female kin [Beehner, 2003; Beehner & Bergman, 2006]. Thus, hybrid females in Group H may have favored males with an intermediate behavioral agenda, who sought permanent bonds with females, yet did not completely isolate them from their female kin. Females, moreover, showed a preference for males whose appearance resembled their own [Bergman & Beehner, 2003], perhaps contributing to the success of the group's phenotypically intermediate males. Additionally, most consortships (74%) in Group H were between partners with a prior history of association [Bergman & Beehner, 2004]. Males thus derived reproductive benefits from investing in relationships with females, even when they were non-estrous. In fact, the three most successful males in Group H habitually associated with females through all phases of their estrous cycle, although the nature of these associations was variable, and in only one case conformed to the hamadryas norm of the OMU. Another male led a "loose" OMU, whereas the third engaged in a form of serial monogamy associating with a female continuously across multiple cycles until she became pregnant, and then moving on to a new female.

In contrast to anubis groups, consort turnover was observed rarely. Although this may be because of the lack of pure anubis males in Group H, it should also be noted that subgroup formation in itself diminishes male ability to monitor female receptivity across the entire group, and thus to carry out the anubis-like male strategy of competing only for estrous females. From the female perspective, subgrouping favors strengthening long-term bonds with males that minimize the risk of predation or infanticide. In chacma baboons, subgroup formation contributed to exclusive mating among subsets of the males and females in a group located in Suikerbosrand, South Africa [Anderson, 1989]. Similarly, we suggest that subgroup formation in Group H also favors males and females that form long-term cross-sex bonds [Bergman, 2006]. The overall picture of Group H is one of an "intermediate" society that combines some anubis-like features with a more flexible version of behaviors seen in hamadryas society. Moreover, male philopatry and the formation of long-term bonds within as well as between sex cohorts, would allow the evolution of an idiosyncratic social structure that may persist over multiple generations. Group H males would probably not be very reproductively successful in less hybridized groups, but might fare better than "pure" immigrants in the unique social context of their natal group. They might also present a united front against the permanent immigration of such indivi-

duals. It is striking that in recent years the majority of natal males remained in Group H, while none of the many phenotypically pure hamadryas and anubis males living within a day's journey of Group H's range have succeeded in immigrating.

The growing success of phenotypic intermediates in Group H may be caused by the increasingly intermediate nature of the group. Group H became more phenotypically and behaviorally intermediate, and less taxonomically polarized between the 1970s and the 1990s, and phenotypic intermediates apparently became more successful over the same interval. Not only do intermediates appear more successful in this study than they did in the 1970s, but intermediate males of the current generation also produced offspring at a higher rate than did previous intermediate males.

It is also possible that the process has been promoted by restructuring of Group H's relatively closed gene pool. The PHI and GHI were tightly correlated among older males, but uncorrelated among males born more recently. This pattern is consistent with earlier males belonging to an early generation of hybrids in which linkage disequilibrium is still strong, whereas males born more recently represent later generations in which recombination has uncoupled the genetic bases of the PHI, the GHI, and behavior. It is also possible that, as in other hybrid zones [Arnold & Hodges, 1995; Barton, 2001; Burke & Arnold, 2001], Group H males with high reproductive success received a particular combination of parental genes that determines a behavioral agenda especially well-suited to the peculiar social context of Group H. Whether this advantage would carry over into less hybridized groups outside the center of the hybrid zone is unknown. Nevertheless, the finding that intermediate males were successful in Group H, strongly suggests that, at a minimum, any selection against hybrid males that exists in the hybrid zone is not an absolute barrier to admixture in the region.

The tension-zone model predicts that a persistent hybrid zone can be maintained by a balance between immigration and low hybrid fitness [Barton & Hewitt, 1985; Key, 1968]. In the purest form of the model, hybrid disadvantage is independent of environment [Barton & Hewitt, 1985] and caused by negative epistatic interactions [Burke & Arnold, 2001]. The results reported here suggest that the Awash hybrid zone is not a classic tension zone, because intermediate phenotypes were not disadvantaged and intermediate behavior was associated with the highest reproductive output (at least in the center of the hybrid zone). However, hybrid males apparently are at a disadvantage in groups where they are a minority, and where hybrid females are few or absent. Across the zone, male reproductive success seems to be determined in a frequency-dependent fashion, with males that match the

majority of the group having the highest success. Phenotypically pure hamadryas and hybrid males living in mostly anubis groups often lose ''their'' females to the more persistent anubis males when the females come into estrus [Beyene, 1998; Nystrom, 1992]. In mostly hamadryas groups, all females are attached to OMUs and lone, immigrant anubis and hybrid males have little opportunity to interact with females [personal observation; Sugawara, 1982, 1988]. The dynamics of the Awash hybrid zone thus appear to mimic ecological selection-gradient (''ecotone'') models [Endler, 1977; Moore & Price, 1993; Slatkin, 1973], but in this case, the transition in the social environment is the key determinant of relative fitness.

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REFERENCES

Alberts SC, Altmann J. 1995. Preparation and activation: determinants of age at reproductive maturity in male baboons. Behav Ecol Sociobiol 36:397–406.

Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Anim Behav 72:1177–1196.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:229–267.

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW. 1996. Behavior predicts genetic structure in a wild primate group. Proc Natl Acad Sci USA 93:5797–5801.

Anderson CM. 1989. The spread of exclusive mating in a chacma baboon population. Am J Phys Anthropol 78: 355–360.

Arnold ML, Hodges SA. 1995. Are natural hybrids fit or unfit relative to their parents? Trends Ecol Evol 10:67–71.

Barton NH. 2001. The role of hybridization in evolution. Mol Ecol 10:551–568.

Barton NH, Hewitt GM. 1985. Analysis of hybrid zones. Annu Rev Ecol Syst 16:113–148.

Beehner JC. 2003. Female behavior and reproductive success in a hybrid baboon group (*Papio hamadryas hamadryas × Papio hamadryas anubis*) [Ph.D. dissertation]. St. Louis, MO: Washington University.

Beehner JC, Bergman TJ. 2006. Female behavioral strategies of hybrid baboons in the Awash National Park, Ethiopia. In: Swedell L, Leigh S, editors. Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. New York, NY: Springer. p 53–79.

Bergman TJ. 2000. Mating behavior and reproductive success of hybrid male baboons (*Papio hamadryas hamadryas × Papio hamadryas anubis*) [Ph.D. dissertation]. St. Louis: Washington University.

Bergman TJ. 2006. Hybrid baboons and the origins of the hamadryas male reproductive strategy. In: Swedell L, Leigh S, editors. Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. New York, NY: Springer. p 81–103.

Bergman TJ, Beehner JC. 2003. Hybrid zones and sexual selection: insights from the Awash baboon hybrid zone (*Papio hamadryas anubis × P. h. hamadryas*). In: Jones CB, editor. Sexual selection and reproductive competition in primates: new insights and directions. Norman, OK: American Society of Primatologists. p 503–537.

Bergman TJ, Beehner JC. 2004. The social system of a hybrid baboon group (*Papio hamadryas anubis × P. h. hamadryas*). Int J Primatol 25:1313–1330.

Bert TM, Arnold WS. 1995. An empirical test of predictions of two competing models for the maintenance and fate of hybrid zones: both models are supported in a hard-clam hybrid zone. Evolution 49:276–289.

Beyene S. 1993. Group-fusion and hybridization between anubis and hamadryas baboons at Gola, Ethiopia. SINET: Ethiop J Sci 16:61–70.

Beyene S. 1998. The role of female mating behavior in hybridization between anubis and hamadryas baboons in Awash, Ethiopia [Ph.D. dissertation]. St. Louis: Washington University.

Brett F, Turner T, Jolly CJ, Cauble R. 1982. Trapping baboons and vervet monkeys from wild, free-ranging populations. J Wildl Manage 46:164–174.

Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. Nature 425:179–181.

Burke JM, Arnold ML. 2001. Genetics and the fitness of hybrids. Annu Rev Genet 35:31–52.

DeVore I, Hall KRL. 1965. Baboon ecology. In: DeVore I, editor. Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart, and Winston. p 20–52.

Endler JA. 1977. Geographic variation, speciation, and clines. Princeton, NJ: Princeton University Press.

Erhart EM, Bramblett CA, Overdorff DJ. 2005. Behavioral development of captive male hybrid cercopithecine monkeys. Folia Primatol 76:196–206.

Gesquiere LR, Wango EO, Alberts SC, Altmann J. 2006. Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. Horm Behav 51:114–125.

Hewitt GM. 1988. Hybrid zones: natural laboratories for evolutionary studies. Trends Ecol Evol 3:158–167.

Jones CB, editor. 2003. Sexual selection and reproductive competition in primates: new insights and directions. Norman, OK: American Society of Primatologists.

Kappeler PM, van Schaik CP. 2004. Sexual selection in primates: review and selective preview. In: Kappeler PM, van Schaik CP, editors. Sexual selection in primates: new and comparative perspectives. Cambridge: Cambridge University Press. p 3–23.

Key K. 1968. The concept of stasipatric speciation. Syst Zool 17:14–22.

Kummer H. 1968a. Social organization of hamadryas baboons: a field study. Chicago: University of Chicago Press. 189p.

Kummer H. 1968b. Two variations in the social organization of baboons. In: Jay PC, editor. Primates: studies in adaptation and variability. New York: Holt, Rinehart, and Winston. p 293–312.

Maestripieri D. 2003. Similarities in affiliation and aggression between cross-fostered rhesus macaque females and their biological mothers. Dev Psychobiol 43:321–327.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655.

Moore WS, Price JT. 1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. In: Harrison RG, editor. Hybrid zones and the evolutionary process. New York: Oxford University Press.

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 TK. 1997. Mitochondrial DNA analysis of intra-specific hybridization in *Papio hamadryas anubis, P. h. hamadryas* and their hybrids in the Awash National Park, Ethiopia [Ph.D. dissertation]. New York: New York University.

Nystrom P. 1992. Mating success of hamadryas, anubis and hybrid male baboons in a ''mixed'' social group in the Awash National Park, Ethiopia [Ph.D. dissertation]. St. Louis: Washington University.

Packer C. 1979. Male dominance and reproductive activity in *Papio anubis*. Anim Behav 27:37–45.

Phillips-Conroy JE, Jolly CJ. 1981. Sexual dimorphism in two subspecies of Ethiopian baboons (*Papio hamadryas*) and their hybrids. Am J Phys Anthropol 56:115–129.

Phillips-Conroy JE, Jolly CJ. 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 JE, Jolly CJ. 1988. Dental eruption schedules of wild and captive baboons. Am J Primatol 15:17–29.

Phillips-Conroy JE, Jolly CJ. 2004. Male dispersal and philopatry in the Awash baboon hybrid zone. Primate Rep 68:27–52.

Phillips-Conroy JE, Jolly CJ, Brett FL. 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 JE, Jolly CJ, Nystrom P, Hemmalin HA. 1992. Migrations of male hamadryas baboons into anubis groups in the Awash National Park, Ethiopia. Int J Primatol 13:455–476.

Phillips-Conroy JE, Bergman T, Jolly CJ. 2000. Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. In: Whitehead PF, Jolly CJ, editors. Old World monkeys. Cambridge: Cambridge University Press. p 321–340.

Ransom TW. 1981. Beach troop of the Gombe. East Brunswick: Associated University Press. 319p.

Slatkin M. 1973. Gene flow and selection in a cline. Genetics 75:733–756.

Smuts BB. 1985. Sex and friendship in baboons. New York: Aldine. 303p.

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 Stud 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.

Trefilov A, Berard J, Krawczak M, Schmidtke J. 2000. Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. Behav Genet 30:295–301.

Woolley-Barker T. 1999. Social organization and genetic structure in a baboon hybrid zone [Ph.D.]. New York: New York University.