HYBRID ZONES AND SEXUAL SELECTION: INSIGHTS FROM THE AWASH BABOON HYBRID ZONE
(*Papio hamadryas anubis x P. h. hamadryas*)

Thore J. Bergman and Jacinta C. Beehner
Department of Biology, Washington University, St. Louis, MO (T.J.B.);
Department of Anthropology, Washington University, St. Louis, MO (J.C.B.)

INTRODUCTION

Ever since the idea was first espoused by Darwin in his classic *The Descent of Man and Selection in Relation to Sex* [Darwin, 1871], the evolutionary importance of sexual selection has been documented within a multitude of species. Comparatively few studies, however, have focused on the impact of sexual selection on populations of naturally occurring hybrid animals, or hybrid zones, particularly among highly social animals such as primates. Sexual selection is potentially very important in hybrid zones for two complementary reasons. First, hybrid zones typically have high levels of variation in both potential mates and competitors for those mates. This provides unique opportunities to observe sexual selection (both mate choice and within-sex competition) and can reveal relationships that might be too subtle to detect over the range of variation found within a single species. Second, the consequences of sexual selection in hybrid zones can have profound impacts for the evolutionary trajectories of the hybridizing taxa. For example, the evolution of mate preference for conspecifics in the face of selection against hybrids may ultimately lead to speciation, a process known as reinforcement [Dobzhansky, 1940, 1951; Barton & Hewitt, 1981; Paterson, 1982; Butlin, 1987; Liou & Price, 1994]. Conversely, mate preference for unusual or migrant animals could increase gene flow between the two populations, causing what otherwise might have been "good" species to merge. Asymmetry between hybridizing taxa in ability to compete for mates can have similar consequences [Barton & Hewitt, 1985; Hewitt, 1988; Paige et al., 1991; Yoshimura & Starmer, 1997; Crespin et al., 1999; Rohwer et al., 2001]. This chapter presents data on mate preference and intrasexual competition from hybrid baboons (*Papio hamadryas hamadryas x P. h. anubis*) located in Ethiopia's Awash National Park as an example of sexual selection and its consequences in primate hybrid zones.
Sexual selection and hybrid zones

Many studies have demonstrated the significance of sexual selection when closely related taxa overlap and potentially interbreed. Mate preference, one aspect of sexual selection, has been shown to play an important role in creating or maintaining diversity for several hybridizing taxa. Female African cichlids (Petrotilapia trewavas) show a clear preference for male color polymorphisms—a preference that may have had an important role in their rapid diversification [van Oppen et al., 1998; Seehausen & van Alphen, 1999]. Currently, female preference for conspecific color patterns in cichlids serves to maintain distinctness where various forms have overlapping distributions [Seehausen et al., 1997; Knight et al., 1998; Seehausen & van Alphen, 1998].

Mate preference plays a similar role in Heliconius butterflies where speciation between Heliconius erato and H. himera appears to have been driven by strong mating preferences associated with divergence in warning coloration. Mate preferences in these butterflies currently maintain their genetic integrity in the face of hybridization [McMillan et al., 1997]. In a marine snail hybrid zone (Littorina saxatilis), strong assortative mating was observed between two ecotypes with respect to size and morph, due in part to female preference. Despite hybridization assortative mating impedes gene flow between the two ecotypes, possibly leading to incipient sympatric speciation [Rolan-Alvarez et al., 1999]. Female preference has also been shown to act at the level of genotype, with females of Mus musculus subspecies (M. m. musculus and M. m. domesticus) preferring the saliva of males with their own genotype at the salivary androgen-binding protein locus. This preference is thought to contribute to isolation between these two subspecies [Talley et al., 2001].

In addition to causing assortative mating, female preference can act in more subtle ways. One example involves hybridization between pied and collared flycatchers (Ficedula hypoleuca and F. albicollis, respectively). F1 hybrids have reduced fitness owing primarily to the almost complete sterility of F1 hybrid females. Female discrimination against heterospecifics results in strong assortative mating (males do not discriminate) [Saetre et al., 1997]. It was also found that collared females that do occasionally pair with the relatively rare pied males have elevated rates of extra-pair paternity, thus resulting in fewer hybrid offspring. Furthermore, females in heterospecific pairs have relatively more male (i.e., fertile) offspring [Veen et al., 2001]. Therefore, it appears that females have several ways of reducing the fitness costs of heterospecific pairings. A similar situation occurs in fur seals (Arctocephalus spp.) that have a resource defense polygynous mating system. Females that breed on territories belonging to heterospecific males have higher rates of extra-territory insemination, resulting in fewer hybrid offspring [Goldsworthy et al., 1999]. Another example occurs in the hybridogenetic Rana lessonae (L) - R. esculenta (E) waterfrog complex. R. esculenta arose as a hybrid between R. lessonae and R. ridibunda. E x E matings produce no viable offspring while L x E matings produce fully viable and fertile E offspring. Female preference matches the unusual system with E females preferring to mate with L males over their own [Abt & Reyer, 1993]. Furthermore, E females reduce their clutch size when mated by E males. This response may be fa-
vored because it allows them to increase their own residual reproductive value through a second mating with an L male in the same breeding season [Reyer et al., 1999].

In some hybrid studies there is no discrimination against heterospecifics. For example, in a butterflyfish hybrid zone (Chaetodon punctatofasciatus x C. pelewensis), females show no preference for males having a conspecific color pattern [McMillan et al., 1999]. Likewise, in some hybrid populations of crickets (Allonemobius fasciatus x A. socius), females do not discriminate between conspecific and heterospecific songs [Doherty & Howard, 1996]. Experiments with artificially deafened and muted fruit flies of the Drosophila melanogaster complex show that hearing the courtship song of a heterospecific male actually increases the likelihood of heterospecific mating in some crosses [Tomaru et al., 2000]. In all of these cases, sexual selection does not appear to limit gene flow and changes in preference are unlikely to have instigated divergence.

Sexual selection has also been shown to contribute to gene flow across hybridizing populations through an asymmetry in the ability to acquire mates. For example, in a mouse hybrid zone (Mus musculus musculus x M. m. domesticus), female preference for odors of one subspecies has led to asymmetric introgression [Christophe & Baudoin, 1998]. In a manakin hybrid zone (Manacus candei x M. vitellinus), one type of secondary sexual plumage is spreading into a neighboring species [Parsons et al., 1993]. Among pure and hybrid manakins, male aggressiveness closely follows plumage, supporting sexual selection as the agent of asymmetric introgression [McDonald et al., 2001]. Likewise, among interbreeding warblers, male Townsend warblers (Dendroica townsendi) have a clear selective advantage over male hermit warblers (D. occidentalis). They are more aggressive, are better at acquiring breeding territory, and are preferred by females of both species, thereby leading to asymmetric character clines [Rohwer & Wood, 1998; Pearson, 2000]. The superiority of Townsend warblers and hybrids has apparently caused the extermination of hermit warblers over a 2000 km strip as the hybrid zone has shifted south over the last 5000 years [Rohwer et al., 2001].

In addition to the pattern of mating, the fitness of hybrids greatly contributes to hybrid zone dynamics. In some hybrid zones, hybrids have fitness equal to or greater than parental forms. In some of these cases, assortative mating has been found, indicating that sexual selection is maintaining distinctions between lineages that lack other barriers to gene flow. In toads (Bufo microscaphus x B. woodhousii), hybrid males are not at a disadvantage in terms of calling effort or consistency, but mating is still strongly assortative [Malmos et al., 2001]. Among Darwin's finches (Geospiza spp.) hybrids often have greater fitness than either parental species, yet mating is strongly assortative [Grant & Grant, 1992]. In this case, hybridization enhances genetic variation and may facilitate evolutionary change [Grant & Grant, 1994], but assortative mating may reduce the likelihood of this occurring. Common buzzards (Buteo buteo) have a plumage polymorphism that is maintained by a strong heterozygote advantage. Despite the higher fitness of heterozygotes, homozygotes mate assortatively, thereby reducing their own fitness. In this case, the buzzards' maladaptive mate choice appears to result from imprinting [Krüger et al., 2001]. Where no
selection against hybrids is found, mate preference for conspecifics could not have evolved by reinforcement and probably predates hybridization. There are other examples of hybrid superiority (or equality) that show no correlation with assortative mating. In a gull hybrid zone (Larus occidentalis x L. glaucescens), hybrids were found to be superior to parental forms because the hybrid males combine adaptive traits (relating to nest sight selection and diet) of both parental species in an intermediate habitat. No evidence of assortative mating was found among pure forms [Good et al., 2000]. In flickers (Colaaptes auratus auratus x C. a. cafer) clutch size and hatching survivorship do not differ among pure, heterospecific, and back-crossed pairings [Moore & Koenig, 1986]. Not surprisingly, there has been no evidence for evolution of premating isolation in over 90 years that the hybrid zone has been documented [Moore & Buchanan, 1985].

Relatively low hybrid fitness is observed in many hybrid zones and is a major component of the tension zone model of hybrid zone stability [Key, 1968; Barton & Hewitt, 1985; Hewitt, 1988; Barton & Hewitt, 1989]. According to this model, the observed stability of many hybrid zones is the result of an equilibrium between selection against hybrid genotypes and migration. In cases where hybrids are less successful in acquiring mates, sexual selection plays a direct role in reduced hybrid fitness. For example, female stickleback fish (Gasterosteus aculeatus complex) show a clear prejudice against hybrid males despite the fact that these males are viable and fertile [Vamosi & Schluter, 1999]. Sexual selection can also play an indirect role if hybrid breakdown occurs in traits that differentiated under sexual selection. In fruit flies (Drosophila melanogaster) it was shown that sexual traits (testis length and area) have undergone more genetic changes and, consequently, show higher divergence and stronger hybrid breakdown between species than non-sexual traits [Civetta & Singh, 1998].

Sexual selection in primate hybrid zones

Hybridization, or at least intergradation, has been observed in many primate taxa [e.g., spider monkeys: Froehlich et al., 1991; macaques: Fooden, 1964; Fooden, 1971; Bernstein & Gordon, 1980; Southwick & Southwick, 1983; Supriatna, 1991; Evans et al., 2001; guenons: Lernould, 1988; Struhsaker et al., 1988; baboons: Kummer et al., 1970; Nagel, 1973; Dunbar & Dunbar, 1974; Phillips-Conroy & Jolly, 1986; Samuels & Altman, 1986; Alberts & Altman, 2001; gibbons: Brockelman & Gittins, 1984]. Fertile matings have been observed, often in captivity, between primate taxa that show extensive genetic divergence [Dunbar & Dunbar, 1974; Shafer et al., 1984; Pelliciari et al., 1988; Jolly et al., 1997]. Despite extensive interfertility, natural hybridization among primates is generally confined to narrow zones, [e.g., Papio hamadryas hamadryas x P. h. anubis: Phillips-Conroy & Jolly, 1986; Papio hamadryas anubis x P. h. cynocephalus: Alberts & Altman, 2001; Macaca maura x M. tonkeana: Evans et al., 2001] or appears sporadically among overlapping taxa [e.g., Theropithecus gelada x Papio hamadryas anubis: Dunbar & Dunbar, 1974]. Although it remains to be determined whether any of these hybrid zones involve evolutionarily significant gene flow, the confined nature of most areas of intergradation suggests that the effect
of selection is to preserve population distinctness. Reduced fertility of hybrids may play a role. For example, male hybrids between *Macaca hecki* and *M. tonkeana* show degenerative features of sperm in terms of the acrosomic system and spermatogenic activity when compared with pure *M. hecki* males [Enomoto, 2001]. However, in cases where hybrids appear to be viable and fully fertile, another explanation is needed. The complexity of primate societies, the subtleties of reproductive competition, and the pervasiveness of mate choice all point to the significance that sexual selection may have as a limitation on gene flow in a primate hybrid zone.

The dynamics of primate hybrid zones may be influenced by several behavioral characteristics of the primate taxa involved. Although there is some evidence of inbreeding depression in wild primates [Alberts & Altmann, 1995], many primate species have evolved mechanisms for inbreeding avoidance. For example, long-term data on sexual behavior in Barbary macaques (*Macaca sylvanus*) reveals a strong mating inhibition between animals that grew up in the same natal group [Kuester et al., 1994]. In this case, only familiarity during early life, not genetic relatedness, is associated with mating indifference. Mechanisms that evolved to avoid kin mating may favor female preference for novel or extra-group males, and such a preference has been observed in several primate taxa [e.g., sifakas: Richard, 1985; ringtailed lemurs: Pereira & Weiss, 1991; guenons: Cords, 1984; Cords et al., 1986; vervet monkeys: Henzi & Lucas, 1980; macaques: Wolfe, 1986; Sprague, 1991; Manson & Perry, 1993; Manson, 1995; Takahata et al., 1999; baboons: Packer, 1979a; Bercovitch, 1991; gorillas: Harcourt, 1978]. Conversely, females may prefer to mate with novel males because they are the most likely to commit infanticide [Hrdy, 1979; Smuts, 1987; Struhsaker & Leland, 1987]. Although potentially an important factor in primate hybrid zones, it remains uncertain whether preference for novel males would extend to heterospecific males in contact zones. In contrast with the novel-male theory, there is also evidence that females prefer males with whom they are familiar [Packer, 1979b; Rasmussen, 1983; Smuts, 1985]; and this preference can outweigh the outcomes of male-male competition [Smuts, 1985; Strum, 1987; Jurke et al., 1995]. Familiarity with males allows females to assess their potential as protectors of infants, and consequently, the selective pressures of predation and infanticide may lead to preferences that limit (or slow) gene flow in hybrid zones. One review reports an approximately equal number of primate studies that showed female preference for novel males and female preference for familiar males [Small, 1989].

There has been very little work on primate hybrid zones addressing the role of sexual selection. A survey of spider monkeys (*Ateles spp.*) found a pattern of morphological intergradation contrasted by sharp demarcations in pelage patterns. Although the actual mechanism behind this pattern of variation has not been investigated, a model of frequency-dependent assortative mating was proposed to explain their results [Froehlich et al., 1991]. According to this model, there is assortative mating with respect to pelage pattern, yet hybrids are not less fit. Consequently, males with an unusual pelage pattern have low mating success, thus blocking the spread of pelage variations, but not other genes. In Suluwesi, hybridization has been observed between *Macaca maurus* and *M. tonkeana* [Supriatna et al., 1990; Supriatna,
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1991]. These macaques differ in mating behavior primarily due to the more intense male-male competition for mates of *M. tonkeana*. Migratory *M. tonkeana* males may outcompete *M. maurus* males for *M. maurus* females resulting in the observed asymmetric hybridization and gene flow [Supriatna, 1991]. A survey of Y-chromosomal, autosomal, and mitochondrial DNA variation recently confirmed that hybridization occurs predominantly between *M. tonkeana* males and *M. maurus* females [Evans et al., 2001]. A study on captive Sulawesi macaques found that animals show stronger interest in projected images of their own species than those of other macaque species, perhaps indicating a visual preference for conspecifics [Fujita, 2001]. Hybridization has also been observed between anubis and yellow baboons in and around Amboseli National Park, Kenya. An anubis male was observed to have high mating success in a group of yellow baboons despite his low rank [Samuels & Altmann, 1986], perhaps indicating a female preference for the anubis male. However, as there were a large number of adult females that were sexually cycling at the time the anubis male entered the group, the mechanism behind his mating success remains unclear.

One of the best-documented primate hybrid zones occurs between anubis and hamadryas baboons in Ethiopia's Awash National Park. Over 30 years of study in the region provide a wealth of background information [e.g., Nagel, 1973; Sugawara, 1982; Phillips-Conroy & Jolly, 1986; Phillips-Conroy et al., 1991; Beyene, 1993] for our study of sexual selection and hybridization between two of the most behaviorally and phenotypically distinct baboons. That such distinct baboons hybridize, emphasizes the taxonomic difficulty of the genus *Papio* [reviewed in Jolly, 1993]. Different types of baboons replace each other geographically, are phenotypically distinct, and (in some cases) are morphologically and behaviorally distinct as well. However, all baboon forms intergrade or interbreed at their boundaries; and thus delimiting species of baboons depends on the species concept used. Based on the propensity to interbreed in the wild, we [following Jolly, 1993] refer to all baboons as subspecies of *Papio hamadryas*. Others prefer to call them separate species [e.g., *Papio hamadryas*, *Papio anubis*, etc., Alberts and Altmann, 2001], while still others separate only hamadryas as their own species (*Papio hamadryas*) and call the other baboons subspecies of *Papio cynocephalus* [e.g., *Papio cynocephalus anubis*, Palombit, this volume]. Although the data we present may impact the application of certain species concepts to baboons, we do not address this issue here. We agree with Jolly [1993] that the data used in deciding how to classify baboons is more important than the decision itself.

**Hamadryas and anubis baboons**

Hamadryas and anubis baboons have very different social organizations and mating behavior. Anubis baboons are distributed across a wide range of habitats and live in multimale-multifemale groups. The core of anubis groups are tightly bonded, natal females that form strict kin-based dominance relations. Anubis males, generally non-natal, compete for and guard only estrous females. Male-male competition for mates is mediated by a linear dominance hierarchy, where dominant males monopolize the matings with the females most likely to conceive [Paterson, 1973; Packer,
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but personality, residency status, and prior relationship are also important determinants of consort success [Strum, 1982, 1987; Smuts, 1985; Sapolsky & Ray, 1989; Sapolsky, 1990, 1991]. Dominant males are usually of "prime" age (approximately 9-14 years old), but not every prime male reaches the dominant position. In both yellow and anubis baboons, consorting pairs are frequently harassed by other males, and consort turnovers are common [Strum, 1982; Berenstain & Wade, 1983; Smuts, 1985], particularly when coalitions of males attack a consorting male [Hausfater, 1975; Packer, 1977; Ransom, 1981; Smuts, 1985; Bercovitch, 1988]. Contributing to or confounding male consort success, females often exert their own choice for a mate through proximity maintenance and soliciting copulations [Packer, 1979b; Smuts, 1985; Bercovitch, 1987, 1991, 1995]. Females who exhibit a preference for an extra-consort male increase the chance of a consort turnover [Smuts, 1985]. It has been proposed that female baboons choose particular males based on characteristics such as rank [Hausfater, 1975; Seyfarth, 1978; Packer, 1979b], novelty [Bercovitch, 1991; Nystrom, 1992], or familiarity [Packer, 1979b; Rasmussen, 1983; Smuts, 1985]. Alternatively, mating with many males may be favored because it confuses paternity and encourages more males to provide protection (from infanticide, predation, or harassment) for the infant [Bercovitch, 1991, 1995].

Hamadryas baboons, on the other hand, are associated with arid habitat, have a multi-level society based on one-male units (OMUs), and are male-bonded [Kummer, 1968; Abegglen, 1984]. Hamadryas OMUs are long-term relationships between a single male and one or more females. These relationships are continuously maintained with an array of stereotyped male behaviors, including threat displays and neck biting, which elicit a following response from the female [Kummer & Kurt, 1965; Kummer, 1968]. Unlike typical female-bonded cercopithecid social groups [Wrangham, 1980], OMU females are believed not to be closely related to each other and, correspondingly, have relatively low levels of within-unit affiliation [Kummer, 1968]. Typically, males "respect" each other's possession of females and there is little overt competition for females, all of whom are integrated into OMUs well before adulthood [Kummer et al., 1974]. However, experiments with both wild and captive hamadryas baboons suggest that the female's preference for her leader male may contribute to the respect that extra-unit males show for OMU bonds [Kummer et al., 1974; Bachmann & Kummer, 1980]. Furthermore, an uncooperative female requires more herding, and is therefore more costly possession than one that prefers her leader male. In such cases, a rival male is more willing to attempt a takeover and, concomitantly, her leader is more willing to give her up [Kummer et al., 1970]. During the turmoil of the occasional OMU takeover, females from a single OMU can be distributed among several OMUs [Swedell, 2000b], and these occasions offer opportunities for males to expand their OMU and for females to seek preferred males.

Although female choice probably plays a greater role in hamadryas society than was previously thought [Swedell, 2000a], it is much more subtle than that which has been observed in anubis societies. The control that hamadryas males exert over females leaves little room for females to object. Only rarely do hamadryas females interact and solicit copulations with extra-unit males [Kummer, 1968; Sigg et al.,
1982; Swedell, 2000a] although hamadryas females do frequently stray from their males and could express preference through proximity maintenance [Swedell, 2000a]. Hamadryas females and their infants receive protection from their leader males [Sigg, 1980; Kummer et al., 1985; Swedell, 2000a; Rohrhuber, 1987 (in German) as referenced in Kaumanns et al., 1989]. Therefore, unlike anubis females, they may not benefit from confusing paternity. Additionally, as OMU takeovers appear to be relatively rare [Swedell, 2000a; Zinner & Deschner, 2000] and often cannot be anticipated by the group females [e.g. following an injury to the leader male: Swedell, 2000b] the threat of infanticide is more sporadic than in anubis societies. Consequently, rather than rely on paternity confusion before a takeover, hamadryas females may have developed an alternative strategy that involves deceptive sexual swellings for dealing with the threat of infanticide following an OMU takeover [Zinner & Deschner, 2000].

In summary, it appears that sexual selection is a predominant force in anubis societies where every estrous female is actively contested. Male-male competition plays an active and obvious role in determining who reproduces and who does not. Sexual selection is perhaps a more subtle and intermittent force in hamadryas societies where bonds between males and females are long-term. Sexual selection in hamadryas groups favors the ability to attract females and prevent them from straying, rather than the ability to compete with other males outright [Jolly, 1963] (Figure 1). It has been proposed that the long silvery mane of the hamadryas male may have evolved to help this ability attract and keep females in close proximity [Jolly, 1963]. Perhaps lending support to this theory, previous behavioral observations of Awash groups with both phenotypically-pure anubis and hamadryas males indicated a slight female preference for hamadryas males (as measured by grooming rates) [Nystrom,
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1992; Beyene, 1998]. That hamadryas and anubis baboons differ in physical appearance, especially with respect to male secondary sexual characteristics, has been well-documented [phenotypic index used by Nagel, 1973; Phillips-Conroy & Jolly, 1986]. With such sharp distinctions between both physical appearance and mating behavior in hamadryas and anubis baboons, there is tremendous potential for sexual selection in the Awash hybrid zone.

Findings from the Awash hybrid zone

The Awash hybrid zone has a predominantly linear arrangement of groups along the Awash River in Ethiopia's Awash National Park. The zone currently spans eight groups that range from nearly pure anubis at the upstream end to nearly pure hamadryas 30 km downstream. Several findings related to sexual selection have emerged from previous studies in the Awash hybrid zone.

1. Male-male competition plays a significant role in the formation of hybrids. Hybridization was originally proposed to occur through hamadryas male "abduction" of unattached females from anubis groups to hamadryas groups where hybridization would then occur [Kummer et al., 1970; Nagel, 1973]. However, this scenario has rarely been observed, nor is it supported by distributions of mtDNA [Bergman, 1997; Newman, 1997]. Most hybridization probably occurs through the cross-migration of males [Sugawara, 1979; Phillips-Conroy et al., 1991; Nystrom, 1992] and through group fusion [Beyene, 1993, 1998]. In both scenarios, hybrids are necessarily formed in groups where different types of males are competing against each other for access to estrous females.

2. Barriers to gene flow in the Awash would most probably be due to ineffective hybrid male mating behavior. In the Awash, several generations of hybrids have been observed, and there is no evidence of any physiological breakdown of hybrid individuals [Phillips-Conroy & Jolly, 1986]. Therefore, any barriers to gene flow that may exist in the hybrid zone would probably be due to behavioral differences in mating strategies [Nagel, 1973; Sugawara, 1979, 1982, 1988]. Previous observations in the hybrid zone have indicated that hybrid males may have somewhat ineffective mating behavior. Sugawara [1988] reported that male hybrids spent considerable time following non-estrous females, attempting to form hamadryas-like permanent relationships with them, only to lose the females to other males when they came into estrus [Sugawara, 1988]. Therefore, it has been proposed that hybrid males may have reduced fitness due to an inability to compete for mates.

3. Female behavior is relatively flexible while male behavior is not. Transplant experiments have shown that, when placed in a group with hamadryas males, most anubis females quickly learn to follow a leader male [Kummer et al., 1970]. On the other hand, hamadryas males living in anubis groups will still attempt to form permanent bonds with any seemingly unattached females [Phillips-Conroy et al., 1991; Nystrom, 1992]. Because males may be behaviorally inflexible, the differences in male mating behavior can be very important in determining the outcome of competition for mates. Earlier work has found that, in the context of a mostly-anubis group with a few resident hamadryas males, anubis males are apparently able to out-com-
pete hamadryas males for access to estrous females [Nystrom, 1992], while in mostly-hamadryas groups anubis and hybrid males have little interaction with any females [Sugawara, 1982]. Therefore, sexual selection may inhibit the success of heterospecific males, but it is not known which type of male would be successful in an evenly mixed group.

The previous findings indicate that the Awash hybrid zone holds a strong potential for sexual selection and that the outcome of this sexual selection may be important in determining gene flow. To further understand sexual selection in the hybrid zone we have undertaken observation of the group at the center of the Awash hybrid zone (Group H). In this paper we address the following questions using three years of behavioral data.

1. Is there female preference for certain males?
2. Is there assortative mating?
3. Which males are most successful in a hybrid group, and why?

METHODS

Study group

The data presented here come from observation and analysis of members of a single group at the phenotypic center of the Awash hybrid zone, Group H. The groups upstream of H are predominantly anubis, and groups downstream are predominantly hamadryas [Nagel, 1973; Phillips-Conroy & Jolly, 1986; Nystrom, 1992; Beyene, 1998; Bergman, 2000]. The current members of Group H are hybrids that cover most of the phenotypic spectrum from anubis to hamadryas [Bergman, 2000]. Group H also encompasses the greatest genetic variation of any group in the hybrid zone [Newman, 1997; Woolley-Barker, 1999]. Analyses of population-specific mtDNA haplotypes show that in both 1973 and 1998 Group H contained approximately equal proportions of anubis and hamadryas haplotypes [Newman, 1997; Bergman, 2000].

Group H was studied by one of the authors (Bergman) from June 1997 until November 1998 and again by the other author (Beehner) from November 1999 until December 2000. For the years that this study was conducted, the group ranged from 15-19 adult males and 27-32 adult females. A male was considered an adult when he was dentally mature, with at least one third molar erupting. Based on dental eruption schedules, such males are believed to be about 98 months old [Phillips-Conroy & Jolly, 1988]. These males showed adequate development of secondary sexual characteristics for the determination of the phenotypic hybrid index score described below. A female was considered an adult once she began to develop full-size sexual swellings, typically about eight months after menarche. As individuals reached adulthood, they were included as subjects in this study. Two males and three females disappeared, one male immigrated, and five males and eight females reached adulthood over the course of behavioral collection, resulting in a total sample size of 21 males and 33 females for analyses.

The social structure of Group H reflects its mixed ancestry with elements of both anubis and hamadryas society. Within the group there were several males who showed
a strong interest in non-estrous females and formed OMUs. We categorized these OMUs as either "strict" or "loose" based on the consistency of the members, the proximity of members to each other, and how often the leader male maintained the unit. Even the OMUs we categorized as strict were not as cohesive as those found in a pure hamadryas society [Bergman, 2000]. Alternatively, there were also several males who had primarily anubis behavior, displaying an interest in females only when they were in estrus. However, unlike many anubis males, they never formed coalitions or harassed the consortships of other males. Females also rarely sought interaction with extra-consort males. Within Group H, both a general "respect" for another male's possession of a female and a female's willingness to stay with a male – both hamadryas traits – seemed to predominate. Levels of male-female bonding among all members of Group H (as measured by grooming interactions and proximity) were intermediate between pure anubis and hamadryas groups [Bergman, 2000]. Male-male interactions on the whole were rare, and those that were observed had no clear "winner" or "loser". Consequently, the males of Group H could not be placed in a linear dominance hierarchy. Both inside and outside of OMUs, females rarely followed males, yet they also rarely sought interaction with extra-OMU or extra-consort males [Bergman, 2000]. For the majority of estrous cycles observed, a female entered a consortship near the onset of swelling and stayed in consort with the same male for the duration of her estrous cycle.

**Phenotypic Hybrid Index Score**

Nagel [1973] first established a system of assigning a phenotypic hybrid index score (or PHIS) for hybrid males based on eight phenotypic traits for which hamadryas and anubis males differ (face color, face shape, cheek tuft color, cheek tuft shape, mane length, anal patch color, anal patch shape, and tail shape). Later, this system was modified to seven traits (face shape was excluded because scores were assigned based on photographs, and too few of them showed the requisite profile [Phillips-Conroy & Jolly, 1986; Phillips-Conroy et al., 1991]). Here, we adopt the system used by Phillips-Conroy and Jolly [1986], but we add an additional trait – mane color. Group H has an enormous amount of variation in mane color; some males have the silvery-gray cape of the hamadryas, while others have the agouti mane of the anubis. All of the above authors score each trait the same. A score of 0 represents the hamadryas condition, a score of 1 represents the intermediate condition, and a score of 2 represents the anubis condition. Because our study focuses on a single group consisting of only hybrid individuals, it was necessary to expand the intermediate category so that a greater range of hybridity could be distinguished. Therefore, we also use partial scores of 0.5 or 1.5 as traits approach the hamadryas or anubis condition, respectively. The scores were summed across all eight traits resulting in a total PHIS of 0 for a pure hamadryas male and a score of 16 for a pure anubis male. In natural "pure" populations, hamadryas males typically range from a PHIS of 0 to 4, and anubis males typically range from 14 to 16 [personal observation]. The male PHIS scores in Group H range from 5 to 15.
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Table I. Number of individuals in each phenotypic group for Group H based on Phenotypic Hybrid Index Score (PHIS).

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<th>Most hamadryas (3.0 - 8.5)</th>
<th>Hamadryas-like (9.0 - 11.0)</th>
<th>Anubis-like (11.5 - 13.5)</th>
<th>Most anubis (14.0 - 16.0)</th>
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<td>Females</td>
<td>6</td>
<td>9</td>
<td>8</td>
<td>10</td>
<td>33</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>15</td>
<td>13</td>
<td>15</td>
<td></td>
</tr>
</tbody>
</table>

a) Numbers under phenotype groups indicate the PHIS range for that group.

Because many of the traits used in the PHIS are secondary sexual characteristics (such as the cheek tufts and mane), fewer traits differentiate the females. Females were assigned a PHIS based on four of these traits: face color, hair color, hair length, and tail shape. For female traits, a score of 0 indicates a pure hamadryas condition and a score of 4 indicates a pure anubis condition so that the female PHIS, like the male PHIS, ranges from 0 to 16. Female PHIS scores in Group H range from 4 to 16.

We then used these PHIS scores to divide up the baboons into four phenotypic groups. Males and females were separately arranged according to PHIS score and then divided into four relatively equal categories. The resulting groups and corresponding PHIS scores are as follows: the most hamadryas group has scores from 3.0-8.5, the hamadryas-like intermediates have scores from 9.0-11.0, the anubis-like intermediates have scores from 11.5-13.5, and the most anubis group have scores from 14.0-16.0 (Table I). Because there are more individuals on the anubis end of the phenotypic spectrum, a larger PHIS range for the hamadryas group is necessary to keep groups evenly weighted. Our goal in assigning these somewhat arbitrary divisions was to pool enough individuals for group comparisons without losing important variation among the phenotypic intermediates. These group divisions are based solely on the scores for Group H and are not meant as a classificatory system for other Awash hybrid baboons [for classification system used across the hybrid zone see Phillips-Conroy & Jolly, 1986].

Although the PHIS is based solely on epigamic characteristics, it was shown to be correlated (p<0.05) with a genetic hybrid index score (GHIS) for the animals from whom we have DNA. The GHIS is based on nine microsatellite loci which are polymorphic in anubis and hamadryas baboons [Woolley-Barker, 1999]. In this study, we use the PHIS instead of the GHIS to represent an estimate of ancestry for several
reasons. First, while the GHIS has the advantage of sampling several neutral loci that are known to be unlinked (all loci are on different chromosomes), the GHIS samples only a small portion of the genome and may not give an overall measure of ancestry. Second, the traits used in the PHIS have been observed to sort independently, are evenly weighted, and are essentially completely diagnostic. Where F1 hybrids were present in an upstream group (Group C), their PHIS scores were around 8 – a score which matches that expected for animals with equal hamadryas and anubis ancestry [personal observation]. Third, using a PHIS allows us to include all animals in the analysis and not just those from whom we have DNA. All the ensuing analyses were performed with both indices, and in no case did the results differ substantively.

**Behavioral observations**

Daily observations on group members included a census of members present, the reproductive stage of all females, and consort status of males and females. Specifically, females were given scores denoting their estrus state as inflating (slight or middle estrus), peak estrus, or deflating. For the purpose of our analyses we wanted to separate females into groups based on likelihood of conception. Therefore, pregnant, lactating, and non-estrous females were all placed in the "non-estrous female" category. Based on neighbor consistency over the course of the day, males were recorded as being alone, with a non-estrous female, an estrous female, or a peak-estrous female. When a male was with a female, she was his nearest female neighbor over 50% of the time, whereas a male that was alone generally did not have any single baboon account for more than 30% of nearest neighbor observations. Any changes in consort status within the day and the conditions surrounding the consort

Figure 2. Hybrid female (PHIS = 4.5) fear grimacing to a hybrid male (PHIS = 13.0). (Photo by Jacinta Beehner.)
change were noted. For some analyses, males were placed in age categories based on dental characteristics such as eruption and wear patterns [Phillips-Conroy & Jolly, 1988; Bergman, 2000]. "Young" males were younger than 9 years old at the end of the study period. "Prime" males were ages 9-14. "Middle-age" males were ages 15-17. "Old" males were age 18 or older.

Hamadryas and anubis males differ in many aspects of their mating behavior (e.g., rate of herding non-estrous females, proximity to and association with non-estrous females, consistency of female neighbors, etc.). Perhaps the greatest difference in these two strategies is evident in how males spent their time when not in consort with an estrous female. In other words, were they with a non-estrous female (as would be the case for a hamadryas male), or were they mainly alone (as would be the case for an anubis male)? In this study, we use the difference in proportion of days associated with non-estrous females from the proportion of days spent alone to measure the "anubis-ness" or "hamadryas-ness" of each male's social agenda. We refer to this as a male's behavioral index. Positive scores indicate more anubis-like behavior, and negative scores indicate more hamadryas-like behavior.

Social behaviors (which for this study include presents, grooming, copulations, and aggressive encounters: Figure 2) were recorded for all animals (male and female) in an all-occurrence fashion [Altmann, 1974] noting both actor and recipient. A present is any occurrence where an individual presents her/his hindquarters to another for inspection or copulation. Consort turnovers were declared each time a female was observed in consort with a different male during the same estrus cycle. Only all-occurrence data were used in the following analyses. However, scan samples were taken on all baboons within sight of the observer every 5 minutes [Altmann, 1974] recording nearest neighbors, thereby providing a record of observation time for each individual. We standardized our all-occurrence data by expressing each behavior as a proportion of total time observed. We did this by dividing all occurrences of the behavior of interest by the total number of scans on that animal. In our results section we express these proportions as frequencies – or number of occurrences per scan sample. For some analyses an estimate of reproductive success was necessary. In the following analyses we use mating success – or the number of consorts for each male that resulted in pregnancy – as our estimate of reproductive success. In Group H, this measure of male mating success was shown to be highly correlated with actual reproductive success using paternity testing \((r^2=0.76, p<0.001)\) [Bergman, 2000]. Therefore, because we only have actual paternity data for about half of all pregnancies, we use male mating success as an estimate of overall success. All observations were recorded using a microcassette recorder and then later transcribed into a computer spreadsheet for analysis.

**Analysis**

We analyze our data for evidence of sexual selection in three sections: patterns of mating, female preference, and male-male competition. In the section on patterns of mating we look for evidence of assortative mating. While differences in spatial or temporal mating patterns (and not sexual selection) may cause assortative mating in
Table II. All Group H males listed by PHIS, type of one-male unit (OMU), and number of female partners in each phenotypic group.

<table>
<thead>
<tr>
<th>Male PHIS</th>
<th>One Male Unit Type</th>
<th>Most hamadryas (3.0 - 8.5)</th>
<th>Hamadryas-like (9.0-11.0)</th>
<th>Anubis-like (11.5-13.5)</th>
<th>Most anubis (14.0 -16.0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>strict</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.5</td>
<td>strict</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.0</td>
<td>strict</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10.0</td>
<td>strict</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>7.5</td>
<td>loose</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>9.0</td>
<td>loose</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>14.0</td>
<td>loose</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.5</td>
<td>none</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>10.0</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10.0</td>
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<td>13.5</td>
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<td>14.0</td>
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<td>14.0</td>
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<tr>
<td>15.0</td>
<td>none</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>15.0</td>
<td>none</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a For OMU males (strict and loose), female partners are members of the OMU; for non-OMU males, they are females with which the male had at least one complete consortship.

b Numbers under phenotype groups indicate the PHIS range for that group.

some populations, for most primates living in the same group assortative mating requires sexual selection. Therefore, we assume that evidence of assortative mating is an indirect indicator of sexual selection. In the section on female preference, we look at two behavioral measures of female preference to see which type of male is preferred and to look for evidence of assortative preferences. In the section on male-male com-

1 The term assortative preference, as distinct from assortative mating, refers to cases where a female exhibits a behavioral preference for a male with a similar phenotype. It does not necessarily mean that they are found in consort with one another.
petition, we look at how male competition relates to individual success. We analyze the relationships between several male attributes: consort turnovers, ancestry, behavior, age, and mating success.

Data were tested for deviations from normality using the Kolmogorov-Smirnov test and found not to deviate significantly from normal (at $p = 0.05$). Analyses of variance (ANOVA) were used to test for differences across several categorical variables (phenotype, behavior, and age). Linear regression and partial correlation analyses were used to test for relationships among non-categorical variables. To test for assortative mating and preference, consorts and behaviors were scored on a grid with male phenotypic categories represented by columns and female phenotypic categories by rows. Chi-square tests were used to test for deviations from random mating (calculated by the product of marginal totals divided by the grand total) across categories.

RESULTS

Patterns of Mating

Table II summarizes the mating patterns for Group H, indicating the PHIS of each male, whether he is an OMU male or not, and the phenotypic group of his consort

Table III. Differences, observed - expected, by phenotype category for (a) All consorts and (b) Consorts resulting in pregnancy.

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Females</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Most Hamadryas</td>
<td>Most Anubis</td>
<td></td>
</tr>
<tr>
<td>a. All Consorts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most Hamadryas</td>
<td>10.30</td>
<td>-6.13</td>
<td>-3.43</td>
</tr>
<tr>
<td></td>
<td>-6.69</td>
<td>3.42</td>
<td>-0.89</td>
</tr>
<tr>
<td></td>
<td>2.17</td>
<td>3.43</td>
<td>-2.33</td>
</tr>
<tr>
<td>Most Anubis</td>
<td>-5.78</td>
<td>-0.72</td>
<td>6.66</td>
</tr>
<tr>
<td>b. Pregnancies</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Most Hamadryas</td>
<td>-1.23</td>
<td>-0.91</td>
<td>1.33</td>
</tr>
<tr>
<td></td>
<td>-0.86</td>
<td>0.74</td>
<td>-0.40</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.72</td>
<td>-0.98</td>
</tr>
<tr>
<td>Most Anubis</td>
<td>1.40</td>
<td>-0.56</td>
<td>0.00</td>
</tr>
</tbody>
</table>
partners (or OMU females). To test for assortative mating within the group, we looked at the relationship between male PHIS scores and the average PHIS scores of his consort partners. Linear regression showed a non-significant relationship ($r^2 = 0.10; p = 0.184$) between the PHIS of each male and his consort partners. To explore the pattern of mating further, consortships were examined across the four phenotype categories. A 4x4 grid was formed with male phenotype categories along the x-axis and female phenotype categories along the y-axis. A score of one was given to each consort pair. If a female was observed with more than one male during her estrous phase, equal scores (summing to one) were given to all consort pairs. Using a chi-square test, we found that the pattern of mating across the four phenotype categories is significantly non-random ($\chi^2 = 31.80, N = 163, p < .001$; Table IIIa). The deviation from random is largely due to an excess of consorts between the most-hamadryas males and females (actual = 23.3, expected = 13). We found that 56% of the consorts of the most hamadryas males are with females from the same phenotype group, despite the fact that these females account for 30% of the estrus cycles. While consorts of the most-hamadryas males are strongly biased towards hamadryas females, the consorts of other males are evenly distributed across phenotype categories. Additionally, there is a fairly strong bias against consortships between the most hamadryas males and the most anubis females (only 9% of the consorts of the most hamadryas males are with anubis females although these females account for 33% of the estrous cycles). Apart from the strong

![Figure 3](image-url)  
Figure 3. Regression analysis of male phenotypic hybrid index score (PHIS) and a behavioral measure of how males spend their time when not in consort, or behavioral index. The behavioral index is scored based on the difference in proportion of days associated with non-estrous females from the proportion of days spent alone. N=21, $r^2=0.22, p=0.03$. 


bias towards hamadryas males mating with hamadryas females, there are few other indications that mating is assortative.

In baboon societies, only a minority of consortships result in pregnancy, so the pattern of reproduction may not reflect the overall pattern of mating. The same chi-square analysis was performed on a subset of 43 consortships that led to pregnancy (as conservatively determined by a cessation of cycling for two months associated with a reddening of the females paracallosal skin). For these consorts, the pattern does not deviate significantly from random ($\chi^2 = 10.51; n = 43, p = 0.31$; Table IIIb). This non-significant deviation from random cannot be explained merely by a smaller sample size, as the deviations from expected are in the opposite direction – towards disassortative mating.

To further explore the conflict between the pattern of mating and the pattern of reproduction, males were separated into successful and unsuccessful males. Successful males are the four males (all of prime age) with the highest numbers of consorts that led to pregnancy (highest mating success). These four males were assigned 28 of the 43 pregnancies observed (65%). When we then looked at only the consorts of the remaining 17 unsuccessful males, we found that these consorts deviate significantly in the direction of assortative mating ($\chi^2 = 31.23; n = 90; p < 0.001$), while the consorts of successful males do not ($\chi^2 = 11.7; n = 73; p = 0.23$). As in the previous comparison, this non-significant deviation from random is in the direction of disassortative mating.

Figure 4. Regression analysis of average consort female PHIS on each male’s behavioral index. N=19 (2 males with 0 consorts were excluded), $r^2=0.28, p=0.02.$
We found a significant relationship between male PHIS and male mating behavior, or behavioral index ($r^2 = 0.22$, $p = 0.03$) (Figure 3). Males who have phenotypes closer to the hamadryas end of the spectrum do indeed tend to act more hamadryas-like, and males who have more anubis phenotypes tend to act more anubis-like. Interestingly, when we looked at this same male behavioral index as it relates to the ancestry of their consort partners, we found that the average PHIS of female consort partners is significantly correlated with the behavioral indexes of the male ($r^2 = 0.28$, $p = 0.02$) (Figure 4) such that males with more hamadryas-like behavior consort with more hamadryas-like females (phenotypically), and males with more anubis-like behavior consort with more anubis-like females.

**Female Choice**

One of the most common measures used to indicate female choice is the frequency of solicits for extra-consort copulations. However, out of 163 cycles observed for Group H, this behavior was only observed twice (by two different females). Other female behaviors which are commonly used to indicate preference include: 1) grooming a male when not in consort, and 2) presenting hindquarters to a male for inspection or copulation. These two measures (termed grooming and presents, respectively) were analyzed to determine if females prefer certain males in Group H. These measures are correlated with each other ($r^2 = 0.40$, $p = .002$) but are presented separately because they may represent different elements of female preference (e.g., presents have a sexual

![Figure 5](image_url)  
Figure 5. Regression analysis of the frequency of presentations that a male receives (the number of times tha a male is presented to by a female per 5 minute scan sample) on his behavioral index. N=21, $r^2=0.48$, $p=0.001$. 


nature while grooming does not). First, we looked at female preference for males in different age groups and found significant differences for presents but not for grooming (one-way ANOVA: grooming, F = 1.29, p = 0.311; presents, F = 5.53, p = 0.008; ). Prime-age males are preferred (in both measures) and either old or young males are the least preferred. Second, we wanted to determine if females show a preference for males of different phenotypes. We found that there is no relationship between preference measures and male PHIS (grooming, $r^2 = 0.008$, p = 0.71; presents, $r^2 = 0.022$, p = 0.52); and this also holds true after controlling for age using partial correlation coefficients (grooming, r = -0.14, p = 0.56; presents, r = -0.29, p = 0.22). There are "preferred" males across the phenotypic spectrum, and interestingly, the most preferred male (on both measures) is an intermediate hybrid (PHIS=8.5). Finally, we wanted to determine if females show a preference for a particular behavioral strategy. We found that female preference measures are correlated with the male behavioral index, in both cases preferring males with more hamadryas behavior (grooming, $r^2 = -0.39$, p = 0.003; presents, $r^2 = -0.48$, p = 0.001, Figure 5) and this is true after controlling for age (grooming, r = -0.61, p = 0.004; presents, r = -0.68, p = 0.001).

<table>
<thead>
<tr>
<th>Table IV. Differences, Observed - Expected by phenotype category for (a) Non-estrous grooming and (b) Presentations.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
</tr>
<tr>
<td><strong>a. Non-estrous</strong></td>
</tr>
<tr>
<td>Most Hamadryas</td>
</tr>
<tr>
<td>----------------</td>
</tr>
<tr>
<td>Most Hamadryas</td>
</tr>
<tr>
<td>27.04</td>
</tr>
<tr>
<td>-22.43</td>
</tr>
<tr>
<td>Most Anubis</td>
</tr>
<tr>
<td><strong>b. Presentations</strong></td>
</tr>
<tr>
<td>Most Hamadryas</td>
</tr>
<tr>
<td>----------------</td>
</tr>
<tr>
<td>Most Hamadryas</td>
</tr>
<tr>
<td>7.00</td>
</tr>
<tr>
<td>1.30</td>
</tr>
<tr>
<td>Most Anubis</td>
</tr>
</tbody>
</table>
To determine if these behavioral measures are then associated with higher male reproductive success, we looked for a significant relationship between each of these variables and number of consorts that result in pregnancy. In this analysis we controlled for male behavior because (as we show in the subsequent section on male-male competition) male mating behavior is significantly correlated with success. Using partial correlation coefficients and controlling for behavioral index, we found that both measures are correlated with mating success (grooming, \( r = 0.60, p = 0.006 \); presents, \( r = 0.50, p = 0.023 \)).

Preference measures were then analyzed for assortative patterns across the four phenotype groups. Using a chi-square test, we found that measures of female preference are not randomly distributed across phenotype categories (grooming: \( \chi^2 = 90.0, n = 940, p < 0.001 \); presents: \( \chi^2 = 39.12, n = 439, p < 0.001 \); Table IV). In each grid, the deviation from random appears to be based on several defining characteristics: an abundance of females in the most hamadryas and the most anubis groups showing preference mainly for males in their own phenotype group. Additionally, there is a clear deficit of females in the most anubis group preferring males from either of the hamadryas groups. Overall, this deviation from random is in the assortative direction.

**Male-male competition**

There was little overt male-male competition for females that could be scored using behavioral measures. In 118 out of 163 cycles observed, the female remained with the same male for the duration of her sexual swelling. Furthermore, in only 5 of the 163 cycles observed was there a consort turnover during the peak-estrus phase. In total, there were 93 incidents of consort turnover recorded during 45 cycles with turnover. In only 7 of these 93 consort turnovers was aggression between two males actually observed. In each of these cases, the male who won the aggressive encounter gained the estrous female. In all other cases of consort turnover, we did not observe the actual turnover itself-only that a turnover had occurred. For the ensuing analyses we make the assumption that consort turnovers are the result of competitive encounters between males. There is the possibility that some of these turnovers may have been initiated by female choice, but we cannot make this distinction based on our data set.

Consort turnovers were analyzed by assigning each male a turnover score. This score was determined by assigning a score of 1 if the female was slight estrus, 2 if the female was middle estrus, or 3 if the female was peak estrus (turnovers among deflating females were not recorded). Winners of turnovers received positive scores and losers received negative scores and all scores were summed. We first investigated whether a male's turnover score is correlated with his mating success. Turnover scores, our measure of male-male competition, are not correlated with male mating success as measured by the number of consorts leading to pregnancy (\( r^2 = 0.11, p = 0.14 \)). We then wanted to determine if turnover scores are correlated with ancestry or age. We found that there is no correlation between male competitive ability and ancestry (\( r^2 = 0.04, p = 0.40 \)). Similarly, a one-way ANOVA across age categories reveals no sig-
Figure 7. Scatter plot of the number of consorts leading to pregnancy (for each male) and the behavioral index of the male. N=21, $r^2=0.23$, p=0.03.

Figure 6. Regression analysis of the number of consorts leading to pregnancy (for each male) and the PHIS of the male. N=21, $r^2=0.001$, p=0.87.
significant differences (F = 0.54, p = 0.66), although prime males do have slightly higher averages than the other three age categories. When we analyzed turnovers specifically across male and female phenotypes, we found that the direction of turnovers deviates significantly from random in a disassortative direction (\( \chi^2 = 49.4, n = 93, p < 0.001 \)). In other words, females are initially in consortships with males phenotypically similar to themselves and are subsequently taken over by males who are less like themselves. The direction of turnover is opposite that of female preference, supporting our assumption that consort turnover is primarily the result of male-male competition.

Access to mating in Group H is not equal for all males. Some males are never associated with estrous females while other males are nearly always in consort with females in estrus. We analyzed the relationships between male ancestry (as measured by the PHIS) and mating success and between male mating behavior and mating success. There is no correlation between ancestry and success – there are successful and unsuccessful males across the phenotypic spectrum (\( r^2 = 0.001, p = 0.87 \), Figure 6). Likewise, we found no differences in mating success across phenotypic categories (F = 0.24, p = 0.87). When we looked at male mating behavior as it relates to success, we found a significant relationship between behavior and success such that males who spend more time associated with non-estrous females, a hamadryas behavior, are more successful (\( r^2 = -0.23, p = 0.03 \), Figure 7). However, as Figure 7 indicates, the most successful males are not the three most hamadryas-like males in terms of the behavioral index, but rather are males more intermediate in behavior.

DISCUSSION

The rarity of overt female choice, male dominance interactions, and consort turnovers suggests that sexual selection plays a less obvious role in the Awash hybrid zone than we expected going into this study. There are several patterns of behavior, however, which do indicate that sexual selection has an impact on the reproductive success of hybrid individuals in the Awash.

Overall, females show no preference for a single male phenotype but do show a strong affiliation for males of their own phenotype (Table IV). Thus, there does seem to be assortative preferences with respect to female choice behaviors. If female preference for males like themselves does, in fact, result in greater mating success for these males, then this would effectively reduce gene flow across the hybrid zone. Because assortative female preference and (to some degree) assortative mating is observed in Group H – a group consisting entirely of hybrids – we think it probable that assortative mating would also be found in mixed groups with pure parental phenotypes, and this is corroborated by evidence for assortative mating in one Awash "fusion" group outside the center of the hybrid zone [Beyene, 1998]. In less-hybridized groups where the phenotypic and genetic differences between individuals is much greater than that of Group H, assortative mating may serve as a significant barrier to gene flow.

There is no evidence that female preference acts against hybrid males or for any type of male. There are preferred males of all phenotypes – the most preferred male
being a phenotypic intermediate. Females prefer prime age males regardless of phenotype. This observation is in contrast with two previous studies of mostly-anubis groups with a few resident hamadryas males that found anubis females have slightly higher grooming preferences for hamadryas males [Nystrom, 1992; Beyene, 1998]. The discrepancy may be attributed to a novel-male advantage that hamadryas males in an all-anubis society might enjoy. On the other hand, there may not actually be a discrepancy between our study and these previous findings. Among Group H females there is a clear preference for hamadryas-like behavior over that of anubis behavior (Figure 5). Consequently, females in these mostly-anubis groups may, in fact, be exhibiting a grooming preference for the behavior of the hamadryas male (rather than his phenotype). Perhaps females are directing their attentions toward the male most likely to respond. In all cases where she is non-estrous (about two-thirds of the time if she is cycling, and all the time during pregnancy and lactation), the male most likely to reciprocate her attentions (all else being equal) is one whose behavior toward females is not significantly altered by estrous state, i.e., the hamadryas males. This hypothesis, of course, does not take into consideration other factors that affect female-male social behavior such as previous consortships, friendships, and relatedness.

Despite the rarity of consort turnover and extra-consort copulation, female preference may still be an important factor in determining a male's paternity success. Males who are preferred by females based on non-estrous grooming and presents had greater mating success. However, the direction of causation for this relationship cannot be determined using our current data set, i.e., females may exhibit a preference for these males because they are successful. Therefore, the link between measures of female choice and evidence for sexual selection remains somewhat ambiguous.

We found no evidence that male-male competition, as measured by consort turnover wins or mating success, leaves hybrid males at a disadvantage. Rather, intermediate phenotypes and behaviors (in terms of association with non-estrous females) are associated with the highest mating success (Figures 4 and 5). The mixed social structure of Group H and the rarity of consort turnover most likely contribute to the success of such intermediate behavior. Three of the four males with strict OMUs have only one female in their OMU and therefore only one female with whom they interact. These males, behaviorally, are very hamadryas-like and also have low mating success. Males at the anubis end of the behavioral spectrum rarely interact with non-estrous females but also rarely consort with females at all. The rarity of consort turnover emphasizes the importance of initiating consorts in the first place, and the majority of consorts are between males and females that have a prior history of association. Males that frequently interact with one of several females – or males with loose OMUs – have the highest mating success. Therefore, the high mating success of behaviorally and phenotypically intermediate males in Group H most likely would not apply to less-hybridized groups in which estrous females are actively contested (anubis groups) or all females are permanently attached to males (hamadryas groups).

Previous work has shown that hamadryas and hybrid males have low mating success in mostly anubis groups [Nystrom, 1992; Beyene, 1998]. These males would attempt to establish long-term bonds with unattached females only to lose these fe-
males to anubis males when they came into estrus. Conversely, in predominantly hamadryas groups where all females are attached to males, anubis and hybrid males were observed to have little interaction and no mating success with females [Sugawara, 1982]. In our study of Group H—an evenly mixed group with intermediate levels of male-female bonding—males with intermediate behavior are the most successful. Therefore, the pattern that emerges across the hybrid zone is one of frequency-dependent selection, where the type of male behavior favored depends primarily on the make-up of the group. More specifically, we propose that it is the level of male-female bonding that determines which type of male behavior is most successful. In mostly anubis groups, where male-female bonds are relatively weak, actively contesting estrous females is a successful mating strategy. In groups with stronger male-female bonds, forming long-term relationships with a subset of the females is favored. Consequently, sexual selection appears to limit gene flow across the hybrid zone but not back-crossing at the center of the hybrid zone.

The ancestry of a consort female has a stronger correlation with male behavior than with male ancestry. In other words, it is likely that the behavior of males (as opposed to appearance) is responsible for the observed assortative pattern of mating. This may explain the excess of hamadryas male-female consorts in Group H. Four of the five phenotypically hamadryas-like males have OMUs, and the females in OMUs are predominantly hamadryas-like in phenotype (Table II). In addition to being associated with a single male, these females show other related characteristics generally attributed to hamadryas females, such as few social interactions with other females and no clear position in the female dominance hierarchy. It has been previously suggested that hamadryas females may respond more favorably to an OMU male's social agenda than an anubis female [Kummer, 1995]. This behavioral preference may be attributed to a predisposition for associating with males over females, or it may be due to their own social history, or both. A history of OMU membership could foster a learned preference for interacting primarily with males while, at the same time, limiting any alliances with other females. Why hamadryas-like females tend to be in OMUs more often than other hybrids is not clear, and this issue certainly warrants further exploration. For the present study, however, it is sufficient to note that the behavior of hamadryas-like males and females drives the overall pattern of assortative mating in Group H.

Interestingly, despite an overall pattern of assortative mating, reproduction in the group is not assortative. This is related to the fact that the few males who are not mating assortatively are the four most successful males, accounting for more than half of the observed pregnancies. Of all males, these males are the most likely to be exerting choice. It appears that successful males are choosing females without regard to phenotype and are perhaps choosing based on availability and likelihood of conception (i.e., parous females). Therefore, unlike females, successful males do not appear to have assortative preferences. That female preference is assortative while male preference is not is consistent with sexual selection theory [Trivers, 1972]. Females have a greater investment in each offspring so that if a reproductive cost to hybridization exists (which, to date, has not been demonstrated in the Awash), it
would have a greater evolutionary impact on females. Consequently, under these conditions females would have a greater interest in avoiding hybridization. The pattern observed here is consistent with the frequently observed pattern of females being the more selective sex in interspecific encounters [Darwin, 1871; Trivers, 1972; Wirtz, 1999]. A recent review [Wirtz, 1999] has developed a theory based on sexual selection to explain another frequently observed pattern – that of unidirectional hybridization (males of one species mating with females of another, but not the reverse). Wirtz proposes that unidirectional hybridization generally results from females of the rare species mating with males of the common species because, in the absence of conspecific males, females sometimes accept allospecific males. The symmetrical nature of the Awash hybrid zone makes it difficult to test for Wirtz’ mechanism. It would be interesting to study Wirtz’ theory in other primate hybrid zones where, unlike in the Awash, females are sometimes found in groups consisting mostly of heterospecific males.

Our analysis of sexual selection in the Awash hybrid zone, based on patterns of mating, female preference, and male-male competition have several implications for gene flow in the region. On the one hand, we have evidence that there is a high potential for symmetrical gene flow across the hybrid zone (no overall female preference for either anubis or hamadryas male phenotypes, no preference for or against hybrid males, a strong preference for prime-aged males regardless of phenotype, and an overall pattern of reproduction that is not assortative). On the other hand, we found several patterns that indicate significant barriers to hybridization may exist in less-hybridized groups (females show a strong preference for males like themselves, the behavior of the males is significantly correlated with the ancestry of their consort partners, and there are an excess of matings among hamadryas-like males and females). Furthermore, outside the center of the hybrid zone, it appears that sexual selection is mediated by social setting to limit heterospecific matings. Consequently sexual selection does appear to limit gene flow in the Awash hybrid zone.

CONCLUSIONS AND PROSPECTS

There are two major conclusions about the Awash hybrid zone that emerge from this study. First, while there appears to be assortative mating in Group H overall, the matings of successful males (accounting for more than half of the pregnancies) are not assortative. Consequently, reproduction in the group is not assortative. Second, sexual selection does not act against hybrids or hybrid behavior in Group H. However, in the context of other less-hybridized groups, we think it probable that sexual selection would both favor conspecific matings and act against hybrids. Therefore, in the Awash, admixture is not limited by sexual selection but gene flow is.

In our study of Group H, we found that sexual selection was less evident at the center of the Awash hybrid zone than we had anticipated. Nevertheless, we found that sexual selection still can act in subtle and significant ways. This emphasizes the potential importance of sexual selection in other primate hybrid zones – even those in which sexual selection is not readily apparent. Additionally, our study demonstrates that sexual selection in primate hybrid zones can be complex and act in contradictory ways. For example, in Group H female preference was assortative, but this pattern
was obscured by the non-assortative preference of successful males. Thus, it is important to uncover the separate effects of male and female preference and the results of intra-sexual competition. Furthermore, as in the Awash, there may be considerable variation in how sexual selection acts across a primate hybrid zone since mate preference and intra-sexual competition will differ with group composition.

Finally, as a result of our work in the Awash, we are left with a few questions about sexual selection in primate hybrid zones that deserve further attention. Does female preference for novel males extend to heterospecific males in hybrid zones, and what is the relative importance of preference for novel males, assortative preference, and preference for familiar males? A behavioral study on a mostly-hamadryas group at the downstream end of the Awash hybrid zone might provide evidence of female preference for anubis-like males. Such a preference, combined with the available evidence of female preference for hamadryas-like males at the anubis end of the hybrid zone, would indicate that females prefer heterospecific or novel males. If, however, females in mostly hamadryas groups prefer hamadryas-like males, this would support our hypothesis that females prefer hamadryas-behaving males regardless of social context.

We found evidence that females preferred mates phenotypically like themselves while males did not. A similar pattern might exist in other primate hybrid zones, particularly when this pattern of preference fits sexual selection theory (i.e., there is a reproductive cost to hybridization). We would also like to see Wirtz' mechanism of unidirectional hybridization investigated further in primate hybrid zones. For example, in a macaque hybrid zone, predominantly unidirectional hybridization has been explained by the greater competitive ability of *M. tonkeana* males over *M. maurus* males. However, it is also possible that female preference plays a role, supporting Wirtz' mechanism. *M. maurus* females may accept *M. tonkeana* males as mates only when *M. maurus* males are rare and the reverse situation (and, consequently, mating) rarely occurs. The interplay of group composition, mate preference, and mate competition across primate hybrid zones deserves further exploration.

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REFERENCES


Good TP, Ellis JC, Annett CA, Pierotti R. 2000. Bounded hybrid superiority in an avian
hybrid zone: effects of mate, diet, and habitat choice. Evol 54:1774-1783.


Hybrid Zones and Sexual Selection


**Dr. Thore Bergman** received his Ph.D. in biology from Washington University in St. Louis, Missouri, under the supervision of Dr. Jane Phillips-Conroy. His dissertation work focused on male reproductive success in the Awash hybrid baboons using both behavioral analysis and paternity testing. Currently, Dr. Bergman has a post-doctoral position at the University of Pennsylvania working with Drs. Robert Seyfarth and Dorothy Cheney studying cognition and communication in wild chacma baboons.

**Jacinta Beehner** is a Ph.D. student in the anthropology department of Washington University (also under Dr. Phillips-Conroy) studying female competition, reproduction, and associated hormonal variation in the Awash hybrid baboons. She has recently completed the steroid fecal analysis for her study in Dr. Patricia Whitten’s laboratory at Emory University and is currently finishing her dissertation. In addition, she is studying the hormonal correlates of rank and aggression in male chacma baboons.