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Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society

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ABSTRACT

Like humans, hamadryas baboons (*Papio hamadryas*) are unusual among primates in having a multilevel social system and stable pair bonds, and are thus a useful model for the evolution of human sociality. While the kinship structure and sex-biased dispersal patterns that underlie human social organization have been extensively elucidated, the impact of these factors on the social system of hamadryas baboons is currently unclear. Here we use genetic analysis of individuals to elucidate the patterns of male and female dispersal across multiple levels of society in a wild population of hamadryas baboons. We characterized 244 members of five hamadryas bands at Filoha, Ethiopia by genotyping one Y-linked and 23 autosomal microsatellite loci and sequencing part of the mitochondrial hypervariable control region I. We found both male and female dispersal to be limited at the level of the band, with more movement of females than males among bands. By integrating long-term behavioral data for Band 1, we also found evidence for male and female philopatry at the clan level. We speculate that male philopatry at the clan level and female dispersal across one-male units and clans may enable both kin-based cooperation among males and the maintenance of kin bonds among females after dispersal. This would mean that, as in humans, kin bonds within both sexes are a core feature of the hamadryas social system, thus contributing to our understanding of the evolution of social organization in humans.

Introduction

Humans are unusual among primates in displaying a hierarchically structured social system, the evolutionary origins of which are unclear. The core unit of human society is a pair-bonded family group, with multiple groups coalescing to form many levels of subsequently larger communities (Rodseth et al., 1991; Hamilton et al., 2007; Layton et al., 2012). Most human societies today exhibit a strong tendency towards female dispersal and male philopatry (Ember, 1978; Murdock, 1981), and kin selection theory would accordingly predict that the only enduring affiliative relationships would occur among males. However, both women and men generally maintain ties with same sex kin. In addition, the evolution of monogamous or polygynous bonds between the sexes was argued by Chapais (2008) to be the key innovation allowing the eventual development of human society from a chimpanzee-like polygynandrous (promiscuous) mating system. Building on work by Lévi-Strauss (1949), he also argued that the pair bond, coupled with reciprocal exogamy, promotes intergroup alliances due to lifelong relationships with dispersed offspring. More recently he extended this model to explain the evolution of the human multilevel social system via the formation of initially weakly bonded aggregates of one-male-unit groups, which then develop into largely monogamous, strongly bonded multifamily groups (Chapais, 2013). Similarly, Rodseth et al. (1991) extended work by Fox (1967) and stressed the crucial importance of exclusive sexual relationships, kin group exogamy and kin group alliances in the

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evolution of hominin social systems and noted the potential development of these features in only one nonhuman primate: the hamadryas baboon (*Papio hamadryas*).

The notion that hamadryas baboons share several key features with humans was further supported by Swedell and Plummer (2012), who argued that, among nonhuman primate societies, only the hamadryas social system simultaneously allows the possibility of the male kin bonding, female kin bonding, and cross-sex bonding that characterize human societies. This makes the hamadryas baboon an especially suitable model for hominin social evolution, adding to the list of possible hominin-cercopithecid analogies (Jolly, 1970; Strum and Mitchell, 1987; Elton, 2006).

Polygynous pair bonds form the core unit of the hamadryas social system: the one-male-unit (OMU). An OMU consists of an adult 'leader' male, one or more associated adult females along with dependent juveniles, and occasional 'follower' males. Clans of multiple OMUs are the next level of organization, while bands consisting of multiple clans that consistently associate are equivalent to the usual mixed-sex social group in other cercopithecoid monkeys (Kummer, 1968; Abegglen, 1984; Colmenares et al., 2006; Schreier and Swedell, 2009). Also in clans and bands are bachelor males, termed 'solitary' males, who associate with one another and with follower males and juveniles until they acquire females and become leader males (Pines et al., 2011).

While theory predicts and observation generally confirms that the predominantly philopatric sex should exhibit a greater degree of social bonding than the dispersing sex (Wrangham, 1980; Sterck et al., 1997; Perry et al., 2008; Langergraber et al., 2009; Smith et al., 2010; Archie et al., 2011), the extent of sex bias in dispersal of hamadryas individuals among the various social units is currently unclear. A few studies note some level of male dispersal at all social levels (Sigg et al., 1982; Phillips-Conroy et al., 1992; Phillips-Conroy and Jolly, 2004), but the permanency of these transfers is uncertain. In a study of Ethiopian hamadryas at Erer Gota, juvenile and subadult males would follow other clans or bands for weeks or months, but most returned to their natal clan when adult (Sigg et al., 1982). Phillips-Conroy and colleagues (1991, 1992) in the Awash National Park, Ethiopia, observed hamadryas male immigrants in olive baboon (*Papio anubis*) groups, which as a different (sub)species represents immigration beyond the band. Some hamadryas males remained in the new group for at least five years and may have dispersed permanently. However, all data from long-term behavioral studies suggest that hamadryas males do not often transfer between clans or bands and are generally philopatric (Sigg et al., 1982; Swedell et al., 2011).

Male philopatry at both the clan and band level could provide for the development of groups of related males and allow cooperation among male kin. Observations of fights between the adult males of different bands suggest that males within bands cooperate in defending their females against foreign males, e.g., by forming a common line of defense (Kummer, 1968, 1995; Sigg et al., 1982; Abegglen, 1984). Coordination of travel among males has been proposed (Kummer, 1968), and males within clans have been suggested to be related based on morphological similarity (Abegglen, 1984). This inference was supported by investigation of a captive hamadryas and hamadryas-cynocephalus hybrid group (Colmenares, 1992), in which clans were only formed between presumed related males with a preference for full and maternal brothers.

In contrast to males, hamadryas females do not disperse voluntarily but rather are coerced by males to change OMU membership, usually several times in their lifetime (Swedell et al., 2011, 2014). While most researchers agree that in hamadryas dispersal is generally female-biased (Kummer, 1968; Sigg et al., 1982; Abegglen, 1984; Swedell et al., 2011), the relative extent of male and female dispersal across the different levels of the social system is currently unclear.

The apparently female-biased dispersal pattern in hamadryas is surprising given that other baboons, and Old World monkeys in general, live in female-philopatric social groups and exhibit much stronger female–female than male–male or cross-sex bonds (Swedell, 2011; Cords, 2012). Hence, female philopatry and strong female intrasexual bonds are generally considered to be ancestral characteristics of *Papio* while the hamadryas social system represents a derived form (Hammond et al., 2006; Jolly, 2009; Zinner et al., 2009; Swedell and Plummer, 2012). In hamadryas, the strongest social bond is the pair bond between a leader male and each of his females (Kummer, 1968; Abegglen, 1984). However, this bond may coexist with other, potentially kin-directed intrasexual bonds in both males and females (Swedell, 2002a; Swedell and Plummer, 2012). It has been suggested that, unlike in humans, hamadryas females are unable to maintain contact with natal kin after dispersal, implying that a fundamental step in the evolution of human sociality was the ability to create group alliances and maintain both male and female kin bonds through the exchange of females (Fox, 1967; Rodseth et al., 1991; Chapais, 2008). A long-term behavioral study at Filoha, however, has shown that more than half of female dispersal events, i.e., takeovers, occur within bands and that a large percentage of takeovers may even occur within clans (Swedell et al., 2011). If this leads to some degree of female philopatry at the level of the band, it would facilitate the maintenance of female kin bonds post-dispersal and explain why hamadryas females appear to maintain kin-based social relationships (Swedell, 2002a) despite dispersal across social units (Sigg et al., 1982; Swedell et al., 2011).

Considering what we know today, the hamadryas social system shows a suite of features that is unique among non-human primates. Multilevel social systems can be found in few other species of primates: Guinea baboons (*Papio papio*), geladas (*Theropithecus gelada*), and the four species of snub-nosed monkeys (*Rhinopithecus* sp.) (Dunbar, 1993; Kirkpatrick and Grüter, 2010; Patzelt et al., 2011; Grüter, 2012; Snyder-Mackler et al., 2012). In geladas and snub-nosed monkeys, as in hamadryas, the OMU is the basic building block of their society and OMUs aggregate to form one or several layers of social structure (Dunbar, 1993; Kirkpatrick and Grüter, 2010). The existence of stable OMUs has been debated for wild Guinea baboons and the stability of male-female pair-bonds in Guinea baboons is currently unclear, but if OMUs do exist, they are not hamadryas-like in that there is no male herding behavior and more flexibility in female behavior (Dunbar and Nathan, 1972; Sharman, 1982; Galat-Luong et al., 2006; Patzelt et al., 2011). Unlike in hamadryas, where higher order groupings are always formed by the same OMUs, group composition is much more fluid in both Guinea baboons and geladas (Dunbar, 1993; Patzelt et al., 2011; Snyder-Mackler et al., 2012). Geladas are strictly female-philopatric (Dunbar, 1993) and, while no information is available for most snub-nosed monkey species, dispersal is likely female-biased in the Golden snub-nosed monkey (*Rhinopithecus roxellana*) (Grüter, 2012; Chang et al., 2014). Interestingly, dispersal in Guinea baboons is likely also female-biased (Kopp et al., 2014).

An exploration of the role of genetic structure in shaping the hamadryas social system, which is seemingly more similar to that of humans than is any other primate species despite great phylogenetic distance (Rodseth et al., 1991; Swedell and Plummer, 2012), has the potential to make great strides towards improving our understanding of the evolution of human societies. Although previous molecular studies examining patterns of dispersal in hamadryas found a signal of female dispersal, these studies did not incorporate information from the hamadryas multi-level structure but instead compared populations that were mostly tens to