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RESEARCH ARTICLE

The Ties That Bind: Maternal Kin Bias in a Multilevel Primate Society Despite Natal Dispersal by Both Sexes

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In many social animals, individuals derive fitness benefits from close social bonds, which are often formed among kin of the philopatric sex. Hamadryas baboons, however, exhibit a hierarchical, multilevel social system where both sexes disperse from their natal one-male-unit (OMU). Although this would seem to hinder maintenance of kin ties, both sexes appear largely philopatric at the higher order band and clan levels, possibly allowing for bonds with same sex kin by both males and females. In order to investigate the possibility of kin bonds in hamadryas baboons, we identified kin dyads in a band without known pedigree information using a large panel of genetic markers: 1 Y-linked, 4 X-linked, and 23 autosomal microsatellites and part of the mitochondrial hypervariable region I. With these data, we performed a kinship analysis while accounting for misclassification rates through simulations and determined kinship among two types of dyads: leader and follower males and female dyads within OMUs. Leader and follower males were maternal relatives more often than expected by chance, suggesting that kinship plays a role in the formation of these relationships. Moreover, maternal female relatives were found in the same OMU more often than expected by chance, indicating that females may be motivated to maintain post-dispersal contact with maternal female kin. Our results suggest that hamadryas baboons can recognize maternal kin and that kin selection has contributed to shaping their complex social system. This implies that an ancestral maternal kin bias has been retained in hamadryas society. Am. J. Primatol. © 2016 Wiley Periodicals, Inc.

Key words: kinship; hamadryas baboon; female choice; affiliation; kin selection

INTRODUCTION

The causes and consequences of dispersal patterns in social animals are important questions in evolutionary biology because they determine the availability of social and reproductive partners and thereby shape opportunities for the effects of kin selection and other evolutionary processes to operate on social evolution [Clutton-Brock & Lukas, 2012; Greenwood, 1980; Lawson Handley & Perrin, 2007; Pusey, 1987]. Dispersal, the tendency of an individual to migrate out of its natal group, is male biased in most mammal species, whereas philopatry, the tendency of an individual to stay in its natal group, is often female biased [Greenwood, 1980; Pusey, 1987]. Female philopatry leads to co-residence among female kin, who tend to exhibit preferential associations that may include overlapping home ranges, close proximity in a resting or feeding context, increased grooming or play, coalitions, communal nursing of offspring, or group fissions and fusions along matrilines [lions, Pusey & Packer, 1994; lemurs, Nakamichi & Koyama, 1997; hyenas, Smith et al., 2010; Wahaj et al., 2004; elephants, Archie et al., 2006; many rodents, review by Silk, 2007; capuchins, Perry et al., 2008]. Such kin associations may be adaptive, enhancing direct

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fitness by increasing reproductive success via prolonged survival or other means [lions, Packer et al., 1991; voles, Lambin & Krebs, 1993; house mice, König, 1994; marmots, Armitage & Schwartz, 2000; capuchins, Fedigan et al., 2008; ground squirrels, Viblanc et al., 2010], whereas at the same time providing inclusive fitness benefits by enhancing reproductive success of relatives [Hamilton, 1964]. Particularly in some female-philopatric Old World monkeys, females may strongly bias their affiliative behavior toward maternal female relatives [pig-tailed macaques, Massey, 1977; rhesus macaques, Kapsalis & Berman, 1996; Japanese macaques, Chapais, 1997; chacma baboons, Silk et al., 1999; yellow baboons, Silk et al., 2006a,b; mandrills, Charpentier et al., 2007, 2012; possibly geladas, Tinsley Johnson et al., 2013; blue monkeys, Cords & Nikitopoulos, 2015] and may engage in potentially costly support of maternal kin in conflicts with other individuals [Kaplan, 1977; Kapsalis & Berman, 1996; Massey, 1977; Silk et al., 2004, 2010a; Wittig et al., 2007].

Maternal siblings in mammals may recognize one another through common familiarity and close association with the mother, an unlikely mechanism for paternal kin recognition in most mammals due to the rarity of male parental care [Clutton-Brock, 1991; Kleiman & Malcom, 1981]. Still, other mechanisms of paternal kin recognition have been suggested, such as phenotype matching or familiarity with same aged peers in groups with high male reproductive skew [Holmes & Sherman, 1983; Langergraber, 2012; Rendall, 2004]. Support for the idea that at least some primate species may recognize paternal kin comes from recent findings that individuals may bias their affiliative and coalitionary behavior toward paternal kin over unrelated individuals, although maternal kin are typically preferred over paternal kin when both are an option [Charpentier et al., 2007, 2012; Schülke et al., 2013; Silk et al., 2006a,b; Smith et al., 2003; Perry et al., 2008; Pfefferle et al., 2014; Watts, 1994; Widdig et al., 2006, 2001].

Although much is known about kin affiliations and possible mechanisms for kin selection in many female-philopatric Old World monkey species, less is known about relationships among kin in male-philopatric primates, which is surprising given that the primate order contains many of the few male-philopatric species of mammals [Lawson Handley & Perrin, 2007]. Howler monkeys, spider monkeys, woolly monkeys, and muriquis show varying degrees of female-biased dispersal and accordingly, varying degrees of male cooperation and affiliative behaviors [reviewed in Di Fiore, 2009; Strier et al., 2015]. In western gorillas, although both sexes may disperse from their natal group, groups led by related silverbacks often range in close proximity to each other and inter-group encounters are frequently peaceful [Bradley et al., 2004]. Studies of kin biases in male chimpanzees have found that maternal brothers have particularly stable bonds and maternal but not paternal brothers engage in affiliative and cooperative behaviors more often than unrelated dyads [Langergraber et al., 2007; Mitani, 2009]. However, close bonds can exist between unrelated male chimpanzees as well [Gilby & Wrangham, 2008; Langergraber et al., 2007]. In contrast to chimpanzees, Guinea baboon males show no evidence of a linear dominance hierarchy, engage in affiliative interactions and display low levels of aggression, but these measures are not significantly correlated with genetic relatedness [Kopp et al., 2015; Patzelt et al., 2014].

Like the chimpanzee, the hamadryas baboon (*Papio hamadryas*) is a primate species generally characterized by male philopatry and female dispersal [Hammond et al., 2006; Hapke et al., 2001; Städele et al., 2015; Swedell et al., 2011]. Hamadryas baboons live in a multilevel society with four distinct levels: one-male units (OMUs), clans, bands, and troops. OMUs consisting of a leader male, one or several adult and subadult females, and dependent offspring form the first level. Males of particular OMUs, along with extra-OMU bachelors called solitary males, associate with each other to varying extents. Groups of preferentially associating OMUs and solitary males, termed clans, form the second level of the society. The third level is the band, which comprises a social grouping of one or more clans in which males jointly defend their females against males of other bands and are visibly cohesive as a consistent social group [Abegglen, 1984; Colmenares et al., 2006; Kummer, 1968; Schreier & Swedell, 2009; Sigg et al., 1982]. Different bands come together on sleeping cliffs at night to form a troop, which is likely not a true social unit but an outcome of bands associating due to the limited availability of cliffs [Abegglen, 1984; Kummer, 1968; Schreier & Swedell, 2009].

Although both sexes disperse from their natal OMU to reproduce, hamadryas are characterized by female-biased dispersal at other levels of the social structure [Hammond et al., 2006; Städele et al., 2015]. In our study population in Filoha, Ethiopia, males are largely philopatric at the level of the band and clan as indicated by higher average dyadic relatedness within than across bands and clans and clustering of Y-haplotypes within bands and clans [Städele et al., 2015]. However, low levels of Y-haplotype sharing between bands and clans as well as behavioral observations of at least temporary dispersal of males into other bands point to some, albeit low, level of male-mediated gene flow [Phillips-Conroy et al., 1992; Sigg et al., 1982; Städele et al., 2015]. Average dyadic relatedness and patterns of mtDNA sharing indicate that females are also largely philopatric at the level of the band, although to a lesser degree than males. A behavioral study of the same population recorded more movement of females among OMUs within rather than between clans and bands over a period of several years [Swedell et al., 2011]. In sum, these findings of a high degree of male as well as female philopatry at the band and possibly clan level may be compatible with post-dispersal association of maternal and paternal kin dyads within each sex.

The unique nature of hamadryas society, however, imposes constraints on how individuals may associate with one another. Most notably, hamadryas females are aggressively herded by their leader males, who restrict female social activity to within the OMU [Abegglen, 1984; Kummer, 1968; Swedell & Schreier, 2009]. Female transfer in hamadryas is in fact an outcome of coercive behavior by males: leader males of OMUs typically acquire females by taking them over, one at a time, from other males, which can lead to females changing OMU membership several times in their lives (secondary dispersal) [Abegglen, 1984; Kummer, 1968; Swedell et al., 2011]. Takeovers can be aggressive, with males fighting over the possession of females (*challenge strategy*); opportunistic when females become separated from their leader males during intra- and inter-band conflicts or when the leader male is injured, ill or old, and weak and not capable of defending his females (*opportunistic strategy*); or lead to the formation of initial units (*IU strategy*) when males acquire their first, usually sexually immature, female(s) [Kummer, 1968; Pines et al., 2011]. In wild populations, established leaders rarely challenge each other's possession of females and takeovers by leaders are mostly opportunistic [Abegglen, 1984; Kummer, 1968; Kummer et al., 1974; Swedell, 2000, 2006], with the IU and challenge strategies usually being employed by solitary and follower males who are first establishing their OMUs [Pines et al., 2011]. Solitary males reside in the band and are not associated with any OMU in particular, whereas follower males are seen in regular close association with one or two OMUs and are usually tolerated in close proximity by the leader males [Colmenares, 1990, 1991; Kummer, 1968]. Follower and leader males display ritualized greetings, called notifications, in which one male presents to another, often accompanied by lipsmacking, and the other male in return lipsmacks, mounts, and/or or touches the genitals of the notifying male [Colmenares, 1991, 1992; Kummer, 1968]. Followers will groom with the OMU's females, but rarely mount females [Swedell, 2006]. Only follower males can form social relationships with mature females of an OMU, and these relationships can lead to peaceful transfers of those females toward the end of the leader male's tenure or after the leader is deposed by another male (*inheritance strategy*) [Kummer, 1968; Pines et al., 2011]. Follower males apparently benefit from their status as followers in that they often acquire more of their leader's females than other males [Pines et al., 2011, 2015]. Leader males also benefit from follower presence, which is associated with longer leader tenure lengths, more females, and higher reproductive output based on observational data [Chowdhury et al., 2015]. If followers and leaders are kin, then both could also benefit via inclusive fitness [Abegglen, 1984; Chowdhury et al., 2015; Colmenares, 1992; Pines et al., 2015].

Unlike in other long-studied baboon species, where philopatric females benefit by close association with same sex kin [Silk et al., 2003, 2009; but see Guinea baboons, Kopp et al., 2015], the primacy of the bond with the leader male and the separation of females from their maternal kin via successive takeovers would seem to preclude a hamadryas female's opportunity to choose same sex associates [Swedell et al., 2014]. However, although it may appear that OMU membership is determined by male behavior alone, it has been suggested that females can influence the outcome of takeovers by subtly influencing male behavior or, more rarely, freely transferring between OMUs with little male resistance [Bachmann & Kummer, 1980; Swedell, 2000, 2006; Swedell & Schreier, 2009]. We recently found higher average dyadic relatedness of females within compared to among OMUs, suggesting a non-random assortment of females into OMUs [Städele et al., 2015]. Furthermore, an observational study specifically focused on female relationships found that females interact with each other at least as much as with the leader male and noted that there is great variability in the strength of these female bonds among dyads, while females also occasionally interact with each other across OMU boundaries [Swedell, 2002]. It thus appears that hamadryas female relationships may be much more differentiated and important than previously appreciated. Although bonds with kin should be harder to maintain for females due to takeovers by males, an intrinsic motivation of females to maintain bonds with female kin might be expected as it is the ancestral cercopithecine condition [Di Fiore & Rendall, 1994; Jolly, 2009; Strier, 1994; Swedell & Plummer, 2012].

In this study, we examine the potential for kin bias in the dyadic associations of male and female wild hamadryas baboons. In particular, we investigate whether pairs of leader and follower males are maternal or paternal kin more often than expected by chance. We then examine whether female maternal or paternal kin dyads are found in the same OMU more often than expected by chance and describe some observed illustrative circumstances that may allow females to associate with female kin in an OMU despite male herding. To achieve this, we conduct an extensive kinship analysis using 23 autosomal, one Y- and four X-linked microsatellites and mtDNA haplotypes. By defining cut-off values for various relatedness parameters as well as specifying conditions for haplotype sharing, we are able to to reliably distinguish among different kinds of kin categories. This type of analysis allows us to determine the kinship of specific dyads as well as to distinguish between maternal and paternal kinship and, therefore, permits insights beyond those that can be gained by assessing average pairwise relatedness alone [cf. Städele et al., 2015].

METHODS

Dyadic Relationship Classification

The genetic data used in this study derive from a recent analysis of the Filoha hamadryas study population in the Awash National Park, Ethiopia [Städele et al., 2015]. In brief, we obtained genotypes of 156 individuals of the habituated Band 1 and 88 individuals from four unhabituated bands genotyped at 23 autosomal, one Y-linked and four X-linked microsatellite loci and 364 bp of the mitochondrial hypervariable region I. Two genotypes typed at less than ten loci were excluded. Fecal samples were collected from Band 1 between 2004 and 2011 and from Bands 2 to 5 in 2010. In Band 1, individuals are individually identified at an age at which they have typically left their natal OMU, so the vast majority of individuals should be post-dispersal in the sense that they are no longer in their natal OMU. Hamadryas OMUs last only as long as an individual leader male maintains control of a number of females with their dependent offspring, which averages just under 6 years, so they are not permanent social units and both males and females usually leave the units prior to sexual maturity [Pines et al., 2015]. Due to the large number of juveniles in this interim stage between the natal OMU (and association with the mother) and a reproductive OMU as a subadult or adult and the difficulty of identifying juvenile individuals, we have not been able to identify individuals consistently from infancy through adulthood and thus do not have pedigree information for any adult dyads. Additional details on sample collection and completeness can be found in Städele et al. [2015].

Sampling procedures have been approved by the Institutional Animal Care and Use Committee of Queens College of the City University of New York. This research was conducted with permission of and following the guidelines of the Ethiopian Wildlife Conservation Authority of Ethiopia and in accordance with the laws of Ethiopia. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. Because our study exclusively relied on non-invasively collected samples and, therefore, did not involve animal handling or testing, we did not violate any regulations of the Deutsches Tierschutzgesetz.

We used genetic data to assess kinship of dyads in our population. It is notoriously difficult to determine categorical kinship with genetic marker data in the absence of pedigree information [Blouin, 2003; Csilléry et al., 2006; Van Horn et al., 2008]. Approaches used need to take into account that the kinship of a dyad can never be determined with absolute certainty and misclassifications are to be expected and the extent of such error should be quantified [Blouin et al., 1996]. In order to identify related dyads in the absence of pedigree information, we devised an approach (Supporting Information, Fig. S1) inspired by analyses done in Langergraber et al. [2007, 2009]. In brief, we (i) performed a parentage analysis (see Supporting Information) and (ii) identified individuals that shared the same mother and/or father as full and half-siblings (see Supporting Information, reconstruction of partial pedigrees). We then (iii) used these known sibling dyads to determine cut-off values for several parameters, that is, several log likelihood ratio values (LODs) and the minimum dyadic relatedness coefficient, for these kinship categories in our population (Supporting Information, Tables SII and SIII). These parameters were calculated in KINGROUP v2 [Konovalov et al., 2004]. The LOD score is the natural logarithmic ratio of a dyad's likelihood to belong to a certain kinship category (primary hypothesis H) and the dyad's likelihood to belong to other kinship categories (null hypothesis H_0). Based on the cut-off values, we determined (iv) false negative, misclassification (detailed below, Table I and Fig. 1) and false positive rates (detailed below, Table II and Fig. 1) by simulation. Finally, we (v) applied the cut-off values determined in step 3 to our same-sex dyads of unknown kinship to assign the dyads to the categories of full siblings or paternal or maternal second degree relatives or unclassified.

Paternal relatives are hereby defined as dyads related via a common male relative that is the father of at least one of the dyad's members and maternal relatives are defined as dyads related via a common female relative that is the mother of at least one of the dyad's members. Second degree relatives consist of half-siblings, grandparent–grandoffspring, and full avuncular relationships. Although many of these second degree relatives are expected to be half-siblings, differentiating half-siblings from other second degree relatives was not possible due to our inability to clearly differentiate generations by age.

Misclassification and false negative rates

In order to determine misclassification rates among the kinship categories and false negative rates for each kinship category, we generated ten sets of 500 pairs each of full siblings, maternal half siblings, paternal half siblings, and cousins in KINGROUP v2 based on our population allele frequencies based on genotypes of individuals of all bands. Using the population haplotype frequencies, we randomly assigned mtDNA haplotypes to

TABLE I. Classification Rates for Male and Female Kinship Categories

	Actual relationship			
Classified as	Full siblings	Maternal second degree relatives	Paternal second degree relatives	Third degree relatives
Female				
Full siblings	**72.5 ± 2.3**	4.5 ± 1.0	0.5 ± 0.3	0.1 ± 0.1
Maternal second degree relatives	7.7 ± 0.7	**40.8 ± 2.2**	5.3 ± 1.0	2.4 ± 0.4
Paternal second degree relatives	–	–	**43.0 ± 2.1**	15.3 ± 2.0
False negative rate	19.8 ± 2.3	54.7 ± 2.4	51.2 ± 2.5	–
Male				
Full siblings	**72.5 ± 2.3**	1.0 ± 0.5	0.6 ± 0.3	0.0 ± 0.1
Maternal second degree relatives	7.7 ± 0.7	**40.8 ± 2.2**	5.5 ± 1.1	1.3 ± 0.6
Paternal second degree relatives	–	–	**42.8 ± 1.8**	4.2 ± 1.0
False negative rate	19.8 ± 2.3	58.1 ± 2.3	51.1 ± 2.5	–

True positive classification rates are in bold. Other rates are misclassification and false negative rates. Means were calculated from ten sets of each 500 full, half sibling and cousin dyads simulated in Kingroup v2. Second degree relatives are half siblings, full avuncular relatives, and grandparent–grand offspring. Third degree relatives are first cousins, half avuncular relatives, and great grandparent–great grand offspring. Rates in percent ± standard deviation.

individuals of paternally related dyads, Y-haplotypes to males in maternally related dyads, and Y- and mtDNA haplotypes to cousins in order to simulate the stochastic sharing of these haplotypes between relatives of these kinship categories. We then applied our cut-off values and conditions on matching haplotypes (see Supporting Information, Determining criteria for the classification of dyads) to each set of a certain kinship category and calculated what proportion of dyads would be misclassified (misclassification rate), what proportion of dyads of a certain kinship category would be categorized as unclassified (false negative rates) and what proportion of dyads of a certain kinship category are correctly assigned to that category (true positive rates). The misclassification, false negative, and true positive rates are shown in Table I and graphically represented in Figure 1.

It is important to note that all dyads not categorized as relatives are categorized as unclassified. They cannot be classified as unrelated due to the high false negative rates and, therefore, include many actually related dyads (Table I). Reducing the false negative rates would have the effect of increasing the false positive rates. In studies aiming to look at the impact of kinship upon behavior, many fewer related than unrelated dyads are expected [Lukas et al., 2005] and it is important to set criteria so that the identified set of related dyads is accurate (low false positive rates) and behavioral preferences may be observed, even if many related dyads are not identified (false negatives). Although we could have established criteria for classifying dyads as unrelated, in this study, we do not explicitly compare related and unrelated dyads in subsequent analyses. Having unclassified dyads is not problematic because the ratio of true positives to false negatives is expected to be the same in the observed data and the permutations.

For dyads identified as female second degree relatives, we also determined whether they could potentially be paternal half-sisters as they would then necessarily share an allele at every X-chromosomal locus. This was particularly useful for paternally related female dyads because we expected that some third degree female relatives (cousins, half avuncular relationships, and great grandparent–great grandoffspring) who do not share mtDNA haplotypes would be misidentified as paternal second degree relatives (Table I). Likewise, we also expect that some third degree male relatives would be misidentified as paternal second degree relatives but our estimated misclassification rate was one-third of that for females (Table I).

Determining the false positive rate

In order to estimate a false positive rate (percentage of dyads that are truly unrelated but are misclassified as kin by our criteria), we used KINGROUP v2 to generate a “null hypothesis” from our set of 242 individuals of all bands by randomly permuting alleles at each locus between individuals. This simulates a set of unrelated individuals with the allele frequencies of the real population. We then randomly assigned band membership and Y- and mtDNA haplotypes drawn from our population haplotype frequencies to these new genotypes keeping the number of individuals the same as in the real bands. We created a set of unrelated male and female X-chromosomal genotypes by permuting alleles between individuals. We then randomly assigned an X-chromosomal genotype to an autosomal genotype. We repeated this ten times and thus created ten simulated sets of 242 unrelated individuals (each of 29,161 dyads) and proceeded to calculate all parameters, conduct the parentage analysis and apply cut-off values as for the real set of individuals. The overall false positive rate for male–male dyads was 0.5% and

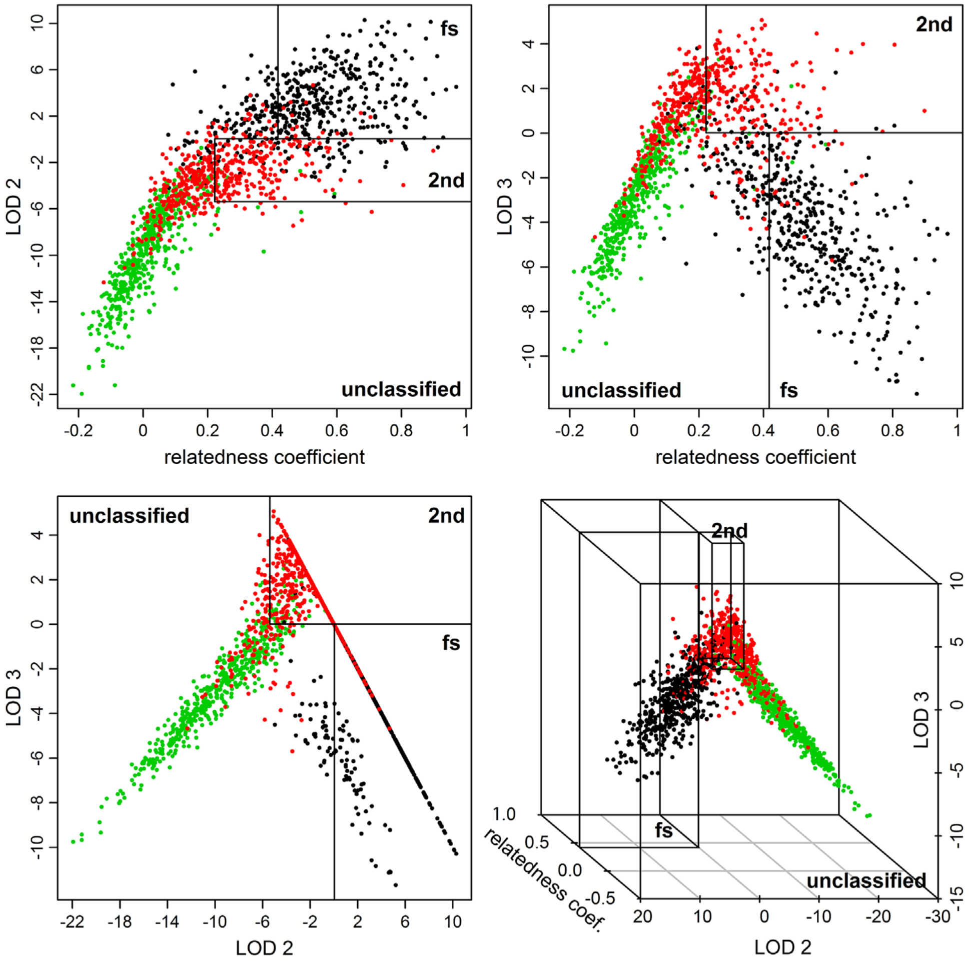

Fig. 1. Graphical representation of dyads in a two- and three-dimensional parameter space. Exemplary sets of 500 dyads of each full siblings (black), half siblings (red), and unrelated dyads (green) simulated from the population allele frequencies in KINGROUP v2. Borders of rectangles and boxes represent the cut-off values beyond which dyads get assigned to a certain kinship category, second degree relatives (2nd), full siblings (fs), or unclassified kinship status. For maternal siblings and full siblings and paternally related males and full brothers, respectively, sharing of mtDNA and/or Y-haplotypes was also required and represents a fourth or fifth dimension not shown. Axes are three genetic parameters calculated from autosomal microsatellite genotypes: coef., coefficient; LOD, natural logarithm of the likelihood ratio of the corresponding parameter; LOD 2, H: full siblings versus H_0: parent–offspring, half siblings, unrelated (autosomal microsatellites; H, hypothesis; H_0, null hypothesis); LOD 3, H: half siblings versus H_0: parent–offspring, full siblings, unrelated (autosomal microsatellites).

1.7% for female–female dyads (Table II). For paternally related second degree female relatives, the rate should be somewhat lower if only potential paternal sisters are concerned because they are also required to share at least one allele at every locus of the X-chromosome. It is important to note that from these rates, we cannot calculate the number of false positive dyads we would expect to find in the final set of related dyads because the actual number of unrelated dyads in the dataset is unknown.

Classification of dyads of unknown kinship

The parentage analysis for individuals of Band 1 and the partial pedigree reconstruction led to the assignment of 113 dyads to categories of known kinship (57 parent–offspring, 28 full siblings, 28 second order relationships), 61 of which were same-sex dyads and 52 of which were cross-sex dyads. Given that a large proportion of both sexes stay in their natal band, finding many related cross-sex dyads is expected. As we were only interested in same-sex dyads, we then applied the cut-off values to all same-sex dyads of Band 1 of still unknown kinship (5,970 dyads). For paternally related second degree female relatives detected in this way, we also checked whether they shared at least one allele at every X-linked locus (parameter 7: P-value < 1; Table SIV). If females did not share one allele at every X-linked locus, they could not be paternal sisters and were rather full avuncular relatives, grandparent–grandoffspring, or third degree relatives that were misclassified as second degree relatives (Table II). All

TABLE II. False Positive Rates per Kinship Category in Simulated Data of Unrelated Individuals

Kinship	Mean expected false positive rate (%)	±SD (%)
Parent–offspring	0.0	0.0
Full siblings		
Female–female	0.0	0.0
Male–male	0.0	0.0
Second degree relatives		
Paternally related, female–female	1.5	0.2
Maternally related, female–female	0.2	0.0
Paternally related, male–male	0.3	0.1
Maternally related, male–male	0.2	0.1

The false positive rate is the percentage of truly unrelated dyads that are falsely classified as kin. Means were calculated from ten datasets of 242 unrelated individuals simulated in Kingroup v2. Second degree relatives are half siblings, full avuncular relatives, and grandparent–grand offspring relationships. SD, standard deviation.

dyads not assigned to a kinship category were considered unclassified, not unrelated, due to the large expected proportion of false negatives given our cut-off values (Table I).

Tests for Non-Random Association

We programmed a permutation test in R 3.0.2. [R Development Core Team, 2013] in order to determine whether females within OMUs and leader–follower male dyads were relatives more often than expected by chance. In order to determine whether leader–follower male dyads were relatives more often than expected by chance, we limited this analysis to the year 2009 because this was the year in which the largest number of leader–follower male dyads were genotyped ($n = 24$, 89% of all individually identified leader–follower male dyads). We included all leader males that did not have a follower male or whose follower male was not genotyped in the permutations ($n = 18$). We then randomly permuted followers among leader males 9,999 times. In order to obtain a *P*-value, we checked how often we found more related dyads in the permutations in comparison to the observed number of related dyads. In some cases, a leader male had two followers or a follower followed two leader males, so in order to avoid pseudoreplication, we chose 20 random subsets of the data in which each male was included in only one dyad and the other dyads it was included in were discarded for each subset. We then ran a set of permutations for each of the subsets. This meant that subsets contained fewer leader–follower dyads than the total number of genotyped dyads ($n = 24$) and also varying numbers of leader–follower dyads ($n = 15$–17). *P*-values are the mean *P*-value of the 20 subsets and the standard deviation. The expected number of dyads is the mean of the 20 permutation means and the standard deviation. In order to investigate whether female relatives were found within OMUs more often than expected by chance we limited this analysis to May 2010, the month in which most females were genotyped (67 females, 65% of individually identified females; 52 within-OMU dyads, 41% of all within-OMU dyads; 35 OMUs). We randomly permuted females among OMUs 9,999 times while keeping the numbers and sizes of the OMUs the same as in the original dataset. In order to obtain a *P*-value, we counted how often the number of female related dyads within OMUs in the permutations was larger than or equal to the observed value.

RESULTS

Dyadic Relationship Classification

We identified 149 male–male and 238 female–female first and second degree relatives among the 156 individuals of Band 1. The number of related dyads identified per kinship category is shown in Table III.

Leader–Follower Dyads

Of the 34 leader–follower male dyads identified between 2004 and 2011 for which genotypes were available, 15 (~44%) were relatives (one parent–offspring dyad, one full sibling dyad, ten maternal and three paternal second degree relatives). The status of eight dyads (~24%) was unclassified, with one dyad sharing an mtDNA haplotype but not a Y-haplotype and seven dyads

TABLE III. Same-Sex Dyads of Kin Identified in Band 1

	Parent–offspring	Full siblings	Maternal second degree	Paternal second degree
Male–male dyads	7	11	40	91
Female–female dyads	18	11	47	162 (73)

Second degree relatives are half-siblings, full avuncular relatives, or grandparent–grandoffspring. Paternally related dyads are related via a common male relative that is the father of one of the dyad's members and maternally related dyads are related via a common female relative that is the mother of one of the dyad's members. The number of paternally related female dyads among all paternal second degree relatives who could potentially be paternal sisters as they share at least one allele at every locus of the X-chromosome is shown in brackets.

sharing a Y-haplotype but not an mtDNA haplotype. Eleven dyads ($\sim$32%) could not possibly have been close relatives because they shared neither Y- nor mtDNA haplotypes. For five (45%) of the follower males in these apparently unrelated dyads, at least one maternal or paternal second degree relative leader male would have been present in Band 1 at the time they started being follower males. In other words, they started following a non-relative leader male despite the fact that a related leader male was present in Band 1 at the time. There were no obvious differences in the number of females or presence of other followers between the OMUs they followed and the OMUs of the related leader males. Only in one case was the leader the father of the follower and the follower's mother was a female in the OMU, so the male likely started following his natal OMU. This dyad was not included in the following analysis because the follower disappeared in 2008. In general, followers are usually older than the average male tenure length of 5–6 years. In all other 14 cases, the leader male could not have been the follower's father. For the 11 leader–follower dyads deemed not closely related, one might argue that the follower was attached to the natal OMU containing his mother and was not related to the leader due to a change in leadership. However, we found that in 8 out of 11 cases, the follower's mother was either in a different OMU ($n = 4$) or none of the OMU females could have been the follower's mother. Only in the three remaining cases were the follower's mother unknown and the followed OMUs incompletely genotyped, so that an untyped female could have theoretically been the follower's mother. It is, therefore, unlikely that the assessment of kinship among leaders and followers was strongly biased due to followers having not yet dispersed from their natal OMU. In 2009, the time with the most individually identified and genotyped leader–follower male dyads, ten dyads were relatives (42% of 24 genotyped leader–follower dyads). These dyads were maternal relatives significantly more often than expected by chance ($P < 0.001$ in all subsets; mean observed number of related dyads in subsets $= 6.0 \pm$ SD 0.7; mean expected number$=0.4 \pm$ SD 0.0; see Methods section). At that time, leader–follower male dyads were not paternal relatives more often than expected by chance ($P = 0.221 \pm$ SD 0.15; observed number $= 1.7 \pm$ SD 0.5; mean expected number $= 0.6 \pm$ SD 0.1).

Female Relatives in OMUs

In order to assess whether females typically have access to female relatives, we investigated how often female relatives were found in the same OMU. We examined data on the composition of OMUs between 2004 and 2010. The number of OMUs in which females were individually identified increased over the years as the number of identifications improved. For example, in January 2004, 55 females in 20 OMUs were individually identified and we obtained genotypes for 28 (51%) of these females, whereas in May 2010, 103 females in 38 OMUs were individually identified and we obtained genotypes for 67 (65%) of these females. For the period between 2004 and 2010, there were ten instances in which we found 11 different dyads of female relatives in the same OMU (8% of 137 different genotyped within-OMU dyads) (Fig. 2). These were four mother–daughter dyads, one dyad of full sisters, one dyad of maternal sisters, three dyads of potential paternal half-sisters, and two dyads of paternally related second degree relatives. In May 2010, the month with the best sampling of females, seven of these dyads were found

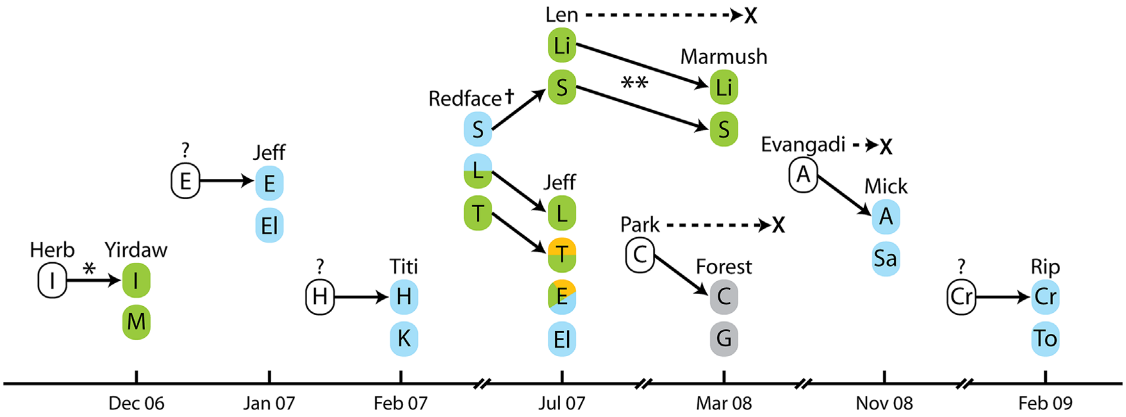

Fig. 2. Transfer of females into one-male-units containing relatives. Females are depicted as ovals below the names of their leader males. Only transferring females and females having a relative in their one-male-unit (OMU) are shown. Solid arrows indicate a female's change of OMU membership. Shared colors indicate a dyad's kin relationship within an OMU (green, mother–daughter; orange, maternal sisters; gray, full sisters; blue, paternal second degree relatives). Paternal second degree relatives are half-sisters, full avuncular relatives, or grandmother–granddaughter where dyads are related via a common male relative that is the father of one of the dyad's members. Dashed arrows indicate the dissolution of an OMU due to death (†) or old age of the leader male (X). ?Leader male unknown. *I is sick and Herb stops herding her. **S changes OMU membership and her daughter Li follows 4 days later.

in the same OMU (13% of 52 genotyped within-OMU dyads). We found that in May 2010, maternally related dyads were found within OMUs more often than expected by chance ($P = 0.016$; observed number of dyads = 4; expected number of dyads = 1.0 ± SD 1.0), but paternally related dyads were not ($P = 0.36$; observed number of dyads = 2; expected number of dyads = 1.3 ± SD 1.1; only potential paternal half-sisters were considered paternally related, see Misclassification and false negative rates section).

We can use observational data to examine the circumstances under which related females ended up in the same OMU. In nine of the ten instances in which female relatives were found in the same OMU, these relatives were not together in the same OMU when they were originally individually identified, but rather one of the females subsequently transferred into the OMU of a female relative (Fig. 2). This means that these relatives were not in the same OMU simply because neither had yet left their natal OMU. In three of these cases, the OMU of origin of the transferring female could not be determined, but in six cases, the transferring females came from OMUs in which the leader died or was ill or old and had begun losing females to other males, which tends to happen relatively quickly near the end of a male's tenure as leader [Kummer 1968; Pines et al., 2015]. In the one remaining case, the transferring female was visibly ill and her leader male had stopped herding her (Herb; Fig. 2). In one instance, a mother and her daughter transferred together into an OMU containing another daughter of that mother after their leader male fell off a cliff and died (Redface; Fig. 2). Another female from this OMU transferred into her daughter's OMU, where they remained together for approximately 8 months (Fig. 2). When the new OMU eventually started to dissolve, probably due to old age of the leader male, the mother transferred into another OMU and the daughter followed 4 days later when the leader male died (Len; Fig. 2). On average, females would have been expected to end up by chance in an OMU with a maternal relative with a likelihood of 0.11 ± SD 0.08.

DISCUSSION

Our analysis of patterns of kinship in a band of wild hamadryas baboons suggests that two important elements of hamadryas society, the relationships among females within an OMU and the relationships between leader males and their followers, are non-random associations of same sex kin. These associations may result from motivations on the part of both sexes to establish and maintain relationships with maternal kin. If so, then kin selection may play a greater role in hamadryas social organization than previously thought.

In this study, leader and follower male dyads were maternal but not paternal relatives more often than expected by chance, suggesting that maternal kinship may play a role in the formation of leader–follower relationships. This is consistent with previous research on captive hamadryas-like hamadryas–cynocephalus hybrids, which found that maternally related leader–follower dyads (either maternal or full brothers) occurred more often than expected by chance while leader–follower dyads were paternal brothers less often than expected by chance [Colmenares, 1992]. Leaders who are at the end of their reproductive career and not likely to sire more offspring could gain indirect fitness benefits by peacefully surrendering mature females to closely related males. Kummer [1968] suggested that old leaders tend to gradually release females from their control. If the females were then taken over by a related follower or ex-follower of the leader, the outcome of this process would be behaviorally similar to levirate or widow inheritance in humans in which a brother marries his deceased sibling's wife, which is practiced in roughly 50% of human societies [Murdock, 1949]. Only follower males are in a position to employ such an inheritance strategy and peacefully and non-opportunistically acquire mature females from other leaders [Pines et al., 2011, 2015]. We do not know the strategy behind the takeovers for enough dyads of known kinship to test whether followers that are related to leaders are more likely to inherit adult females than unrelated followers. Nevertheless, it has recently been shown that OMUs with one or more followers produce three times as many offspring as OMUs without followers due to prolonged leader and female tenures and the acquisition by leaders of twice as many females during their tenure [Chowdhury et al., 2015]. Thus, assuming, as behavioral evidence suggests, near exclusive paternity certainty for leader males, the presence of followers appears to increase a leader's direct fitness and consequentially a related follower's indirect fitness [Chowdhury et al., 2015].

Follower males are in fact unlikely sires of offspring as only ~3% of copulations involve followers and copulations between followers and reproductively mature females are usually incomplete [Kummer 1968; Nitsch et al., 2011; Swedell & Saunders, 2006; Swedell unpublished data]. However, a low probability of paternity may be part of the reason why followers follow even if they are not closely related to the leader. Followers form social bonds with their leader's females and it is likely easier for a follower to take over a female that has a predisposition to join him [Pines et al., 2011]. Generally, followers and ex-followers are more successful in taking over females from their leader or ex-leader than are leader or solitary males [Pines et al., 2011, 2015]. Overall, our finding that at least one-third of assessed leader–follower dyads in this study were unrelated suggests that such relationships are not wholly determined by kinship between the males. In part, the tolerance of leader males toward followers may be explained by disinterest of the leader male in immature natal females who are his probable daughters. Indeed, leader males rarely intervene in interactions between immature females and non-leader males [Abegglen, 1984]. Inbreeding avoidance could, therefore, partly account for the gradual and mostly non-aggressive formations of initial units with immature females by followers. We do not know whether solitary males and unrelated followers are more likely to be tolerated when natal juvenile females are present, but this possibility is supported by the finding of a correlation between the number of followers and the number of pregnant and immature females in an OMU [Swedell, 2006].

We conclude that leader and follower males may both gain direct fitness from their relationship, although the reproductive benefits to followers are delayed rather than immediate. This is complemented by a gain of indirect fitness for both if followers and leaders are related. Whether a male becomes a follower and which leader he follows probably depends on various factors such as kinship to the leader, age, and reproductive state of the OMU's females or the age and physical condition of himself and the leader males in his clan.

The second set of results from these analyses suggests a role of kinship in relationships among hamadryas females. Traditionally classified as a "non-female-bonded" taxon because females disperse among social units and show a lower degree of female–female affiliation than in other baboons, hamadryas females have traditionally been thought to not reside with their kin nor have any motivation to do so. Hamadryas differ from most other female-dispersing taxa, however, in that females are usually forcibly moved between social units by leader males and do not generally appear to be inherently motivated to leave their natal units [Abegglen, 1984; Swedell, 2002, 2006; Swedell et al., 2011]. Behavioral data from Filoha, in fact, show that adult females of the same OMU interact affiliatively (i.e., groom and sit within 10 cm) with each other on average at least as much as each does with her leader male, and that female dyads vary greatly in the strength of these affiliative behaviors, possibly reflecting differences in kinship among dyads [Swedell, 2002, 2006]. The fact that some female–female dyads within the hamadryas OMUs in this study are maternal kin raises the potential for kinship and nepotism to play a role in shaping female social interactions. In this study, for the year 2010, the year with our best sample of females, we found maternally but not paternally related females in the same OMU more often than expected by chance. This non-random association of maternal female relatives in OMUs is best explained by a tendency of females to preferentially join OMUs containing maternal relatives. Some degree of female choice in OMU membership has previously been suggested [Swedell, 2000, 2006], a notion supported by observations of pairs of females, including mother–daughter dyads, interacting across OMUs [Abegglen, 1984; Swedell, 2002] as well as transfers of females who had previously been in an OMU together into the same new OMU directly after one or more changes of OMU membership [Chaylan et al., 1994; Sigg et al., 1982; Swedell, 2000]. An examination of the instances of female transfer into OMUs containing female kin in this study revealed that in all instances in which the OMU of origin was known these transfers occurred in certain circumstances: either the leader died, the female was sick and the leader stopped herding her, or the OMU dissolved during or shortly after the transfer of the female because the leader male lost one female relatively soon after another (which tends to happen to older or ill leader males who cannot effectively herd or defend their females). This suggests that under certain conditions females may be able and motivated to choose membership in an OMU containing female kin and that some opportunistic takeovers may rather be opportunistic voluntary transfers. Although these circumstances arise stochastically and many females may never be found in an OMU with a female relative, females remaining in their natal band in particular should have the opportunity to transfer with or be reunited with a female relative in the same OMU at some point in their lives and occasional interactions across OMUs might represent an additional way of maintaining contact with female kin. Taken as a whole, our results suggest that hamadryas baboon females may have retained an ancestral tendency to preferentially associate with maternal female kin and so instances of female philopatry may not simply be a consequence of a tendency of males to take over females within their band or clan.

Chapais [2001] noted that kin selection might not be the only ultimate driving force behind primate matrilineal nepotism. He suggested that the proximity correlate, the fact that proximity often correlates with matrilineal kinship in female philopatric species, can create matrilineal nepotism in the absence of kin selection. Under the assumption of a proximity correlate, proximity among all kinds of maternal relatives is mediated through the special bonds of mothers and daughters and not through an attraction of other kinds of maternal kin to each other. Nepotistic behavior among these kin could then be driven by natural selection rather than kin selection. The hamadryas social system lacks the proximity correlate due to takeovers of females and, therefore, presents an ideal system for further investigation of these ideas. Our current sample size does not allow us to test whether females transfer into OMUs containing non-mother–daughter relatives at a similar rate as into OMUs containing a mother or daughter. If this were the case and hamadryas females actually displayed nepotistic behaviors, kin selection rather than natural selection acting on individuals in close proximity would explain matrilineal nepotism. Furthermore, this means that matrilineal nepotism would likely also be driven by kin selection in other baboon species. Four out of the five transfers that led to maternal female relatives' being found in the same OMU involved mother–daughter dyads. Studies in other baboons and rhesus macaques have indeed found that mothers and daughters form particularly stronger and more equitable bonds than other female maternal relatives [Schülke et al., 2013; Seyfarth et al., 2013; Silk et al., 2006a].

Ultimately, future research is needed to extend these results beyond mere presence of kin in the same social unit so as to examine if and to what extent hamadryas females bias affiliative social behavior toward related maternal females over unrelated females, as well as whether such biases are adaptive in terms of inclusive fitness benefits in addition to possible direct fitness benefits gained through close social bonds [Silk, 2007]. Research in other cercopithecines has linked strong social bonds among female baboons and mandrills to a younger age at first reproduction, enhanced offspring survival, and increased longevity, and such bonds are preferentially formed with maternal kin [Charpentier et al., 2012; Silk et al., 2009, 2010b].

Our findings of a non-random association of maternal but not paternal dyadic kin, both with regard to female dyads and leader–follower male dyads, is notable considering that the lengthy tenure of leader males combined with seemingly high paternity certainty would appear to facilitate recognition of paternal siblings as well as of father and offspring. Additionally, we previously found Y-haplotypes to cluster within clans suggesting that clans consist of patrilineally related males [Städele et al., 2015]. However, our finding of random association of paternal kin is consistent with findings in many other species in which paternal kin either are not recognized or maternal kin are preferred over paternal kin [Chapais, 1997; Charpentier et al., 2012; Langergraber et al., 2007; Schülke et al., 2013; Silk et al., 2006a; Widdig et al., 2006].

In sum, the social system of hamadryas baboons offers a unique opportunity to investigate maternal and paternal kinship in both sexes due to the co-residence of kin resulting from limited dispersal of both sexes [Städele et al., 2015].

Our results of non-random associations of maternal kin suggest that individuals may recognize and preferentially associate with kin and that kin selection may have played an important role in the evolution of the hamadryas social system. Future research is needed to show whether associating with kin results in inclusive fitness benefits for individuals and, if so, which proximate mechanisms are involved. Furthermore, the tendency of females to join OMUs containing female kin when possible indicates that female bonds, although not immediately apparent, may also be important for hamadryas females. These results corroborate previous hypotheses suggesting that hamadryas baboons occupy an extreme position along a Papionin behavioral continuum [Alberts & Altmann, 2006; Henzi & Barrett, 2003].

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