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Genetic ancestry predicts male–female affiliation in a natural baboon hybrid zone

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Opposite-sex social relationships are important predictors of fitness in many animals, including several group-living mammals. Consequently, understanding sources of variance in the tendency to form opposite-sex relationships is important for understanding social evolution. Genetic contributions are of particular interest due to their importance in long-term evolutionary change, but little is known about genetic effects on male–female relationships in social mammals, especially outside of the mating context. Here, we investigate the effects of genetic ancestry on male–female affiliative behaviour in a hybrid zone between the yellow baboon, *Papio cynocephalus*, and the anubis baboon, *Papio anubis*, in a population in which male–female social bonds are known predictors of life span. We place our analysis within the context of other social and demographic predictors of affiliative behaviour in baboons. Genetic ancestry was the most consistent predictor of opposite-sex affiliative behaviour we observed, with the exception of strong effects of dominance rank. Our results show that increased anubis genetic ancestry is associated with a subtle, but significantly higher, probability of opposite-sex affiliative behaviour, in both males and females. Additionally, pairs of anubis-like males and anubis-like females were the most likely to socially affiliate, resulting in moderate assortativity in grooming and proximity behaviour as a function of genetic ancestry. Our findings indicate that opposite-sex affiliative behaviour partially diverged during baboon evolution to differentiate yellow and anubis baboons, despite overall similarities in their social structures and mating systems. Furthermore, they suggest that affiliative behaviour may simultaneously promote and constrain baboon admixture, through additive and assortative effects of ancestry, respectively.
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Social relationships, both within and between sexes, are ubiquitous features in the lives of social mammals. Affiliative interactions among members of the same sex are positively associated with fertility or survival in a number of social mammal species, including group-living primates, equids, cetaceans and rodents (e.g. Cameron, Setsaas, & Linklater, 2009; Ellis, Snyder-Mackler, Ruiz-Lambides, Platt, & Brent, 2019; Frère, Krützen, Mann, Connor, et al., 2010; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk et al., 2009; Silk et al., 2010; Weidt, Hofmann, & König, 2008). Opposite-sex affiliative bonds can also have important consequences. In monogamous species, strong social bonds between sexual partners predict shorter interbirth intervals, increased offspring number and improved offspring survival, potentially due to improved coordination between partners in caring for young, obtaining resources or defence against predators (e.g. Black, 2001; Griggio & Hoi, 2011; Ribble, 1992; Sánchez-Macouzet, Rodríguez, & Drummond, 2014). Furthermore, in some group-living primates, females compete for access to males outside of mating contexts, suggesting that social bonds with males are themselves an important resource (Archie, Tung, Clark, Altmann, & Alberts, 2014; Baniel, Cowlishaw, & Huchard, 2016, 2018; Cheney,

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Silk, & Seyfarth, 2012; Haunhorst, Fürtbauer, Schülke, & Ostner, 2019; Lemasson, Palombit, & Jubin, 2008; Palombit, Cheney, & Seyfarth, 2001; Seyfarth, 1978). In support of this idea, females in several cercopithecine monkey species benefit from opposite-sex social bonds via enhanced survival, care for their offspring and protection from harassment (Archie et al., 2014; Baniel et al., 2016; Haunhorst, Heesen, Ostner, & Schülke, 2017; Kulik, Muniz, Mundry, & Widdig, 2012; Lemasson et al., 2008; Moscovice, Heesen, Di Fiore, Seyfarth, & Cheney, 2009; Nguyen, Van Horn, Alberts, & Altmann, 2009; Palombit, Seyfarth, & Cheney, 1997; Seyfarth, 1978; Silk, Städele, Roberts, Vigilant, & Strum, 2020; Weingrill, 2000). Males of these species may also benefit from social bonds with females. For example, baboon males who form strong social bonds with females tend to live longer than those who do not (Campos, Villavicencio, Archie, Colchero, & Alberts, 2020). Males may also benefit by gaining mating opportunities (although the evidence for this benefit is mixed), opportunities to care for their offspring or access to infants that can be exploited for social gain (Ménard et al., 2001; Packer, 1979b; Smuts, 1985; van Schaik & Paul, 1996; Whitten, 1987).

While a number of studies have investigated the sources of variance in same-sex affiliative relationships in group-living mammals (Best, Dwyer, Seddon, & Goldizen, 2014; Frère, Krützen, Mann, Watson-Capps, et al., 2010; Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009; Möller, Beheregaray, Harcourt, & Krützen, 2001; Seyfarth, 1976; Seyfarth, Silk, & Cheney, 2014; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; Smith, Memenis, & Holekamp, 2006; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001), we know comparably less about the sources of variance in opposite-sex relationships, especially outside the mating context. Addressing this gap is important for understanding the evolution of heterosexual bonds. In particular, if the tendency to form opposite-sex social bonds is affected by genotype, then it has the potential to evolve in response to natural selection. Strong evidence for genetic effects comes from interspecific comparisons between pair-bonded and multiply mating species. For example, comparisons between the monogamous prairie vole, *Microtus ochrogaster*, and other, closely related promiscuous voles have identified genetic divergence in the pathways that regulate arginine vasopressin, oxytocin and dopamine signalling, which in turn influences pair-bonding behaviour (Young, Huot, Nilsen, Wang, & Insel, 1996; Young, Nilsen, Waymire, MacGregor, & Insel, 1999; Young, Waymire, et al., 1997; Young, Winslow, et al., 1997; reviewed in: Carter & Perkeybile, 2018; Johnson & Young, 2015; Sadino & Donaldson, 2018; Young, Gobrogge, Liu, & Wang, 2011). These pathway differences may in part be due to differences in the distribution and densities of hormone receptors in the brain, suggesting one important mechanism through which variation in opposite-sex social relationships evolves (Insel, Wang, & Ferris, 1994; Insel & Shapiro, 1992; Smeltzer, Curtis, Aragona, & Wang, 2006). Research in other pair-bonded rodents, primates, fish, frogs and birds has placed these findings in a broader context, indicating that these and other pathways (e.g. Young et al., 2019) consistently influence pair bonding across divergent species, although they may do so in a species-specific manner (reviewed in: Carter & Perkeybile, 2018; Fischer, Nowicki, & O'Connell, 2019; Johnson & Young, 2015).

Despite these important discoveries in pair-bonded species, little is known about genetic influences on opposite-sex social bonding in group-living animals, including the degree to which genotype contributes to differences between species with similar social and mating systems. Here, we investigate the association between genetic ancestry and male–female affiliative behaviour in a well-studied natural primate population, the baboons of Kenya's Amboseli basin (Alberts, 2018; Alberts & Altmann, 2012). Baboons (genus *Papio*) began speciating ~1.4 million years ago, and today, the six extant species occupy distinct geographical ranges across Africa (Rogers et al., 2019). Most species of baboons, including those in Amboseli, live in multimale, multifemale social groups in which multiple individuals of both sexes mate and form social bonds (Fischer, Higham et al., 2019). Amboseli lies in a hybrid zone between two such species, the yellow baboon, *Papio cynocephalus*, and the anubis baboon, *Papio anubis* (also known as the olive baboon) (Alberts & Altmann, 2001; Samuels & Altmann, 1986; Tung, Charpentier, Garfield, Altmann, & Alberts, 2008; Wall et al., 2016). While yellow baboons contribute the majority of genetic ancestry in this population, the range of admixture we observe – a continuous distribution from animals that are almost entirely yellow to those that are almost entirely anubis – gives us the opportunity to examine potential genetic ancestry effects on opposite-sex affiliative relationships. Complementary data on social and demographic variables for the same individuals allow us to place these effects in the context of other, environmental sources of variance.

Genetic Ancestry Effects on Male–Female Interactions in Hybrid Zones

The Amboseli baboon hybrid zone provides a 'natural laboratory' for understanding the relationship between genetic ancestry and affiliative behaviour because it allows individuals with varyingly admixed genomes to be observed in a shared environment (Hewitt, 1988). In turn, studying social behaviour in hybrid zones can shed light onto hybrid zone dynamics, as most clearly illustrated in cases where ancestry influences mating behaviour. In such cases, assortative mating by ancestry limits gene flow and can reinforce species boundaries, whereas ancestry-related mating advantages can lead to asymmetric gene flow and range expansion (e.g. Baldassarre, White, Karubian, & Webster, 2014; Baldassarre & Webster, 2013; Kronforst et al., 2006; Mavárez et al., 2006).

Ancestry effects on mating behaviour have also been detected in both the yellow baboon–anubis baboon hybrid zone in Amboseli and in an anubis baboon–hamadryas baboon hybrid zone (*Papio anubis* × *Papio hamadryas*) in Ethiopia. In Amboseli, anubis-like males are more likely to obtain consortships (extended mate-guarding associations between an adult male and an adult female in oestrus, during which most conceptions occur), and male–female pairs with similar genetic ancestry are more likely to consort than pairs with different ancestry (Tung, Charpentier, Mukherjee, Altmann, & Alberts, 2012). In the Ethiopian hybrid zone, ancestry affects both male mating strategy and how females respond to males, and nonoestrous females assortatively groom phenotypically similar males in at least some demographic contexts (Bergman & Beehner, 2003). However, significant gaps remain in our understanding of how genetic ancestry affects male–female affiliation outside of the mating context (but see Bergman, Phillips-Conroy, & Jolly, 2008 for an analysis of male interest in nonoestrous females). If such effects occur, genetic ancestry effects on male–female social relationships may be more important than indicated by analyses of mating behaviour alone. Specifically, because opposite-sex social affiliation also predicts life span in the Amboseli population (Archie et al., 2014; Campos et al., 2020), ancestry effects on this trait may secondarily affect how long individuals live and who they co-reside with, thus influencing the genetic composition of subsequent generations.

Goals of This Study

Here, we evaluated the extent to which genetic ancestry predicts the formation of male–female social relationships in baboons.

We focused specifically on male–female affiliative behaviour in nonmating contexts (i.e. periods when females were pregnant or lactating and not sexually cycling) because social relationships in these contexts are not driven by immediate sexual interactions. Using two multivariate models (one for grooming behaviour and one for proximity behaviour), we simultaneously tested for (1) the additive effects of male and female individual characteristics, including genetic ancestry, on the probability of affiliative social behaviour between males and females, and (2) characteristics defined by the pair, including ancestry-related assortativity. In the same model, we also tested two additional hypotheses: (3) that opposite-sex affiliation depends on female reproductive state (i.e. pregnancy or lactation), based on evidence that the stability of male–female relationships varies across baboon species as a function of female reproductive state (Baniel et al., 2016; Fischer et al., 2017; Goffe, Zinner, & Fischer, 2016; Nguyen et al., 2009; Städele et al., 2019; Weingrill, 2000); and (4) that opposite-sex affiliation depends on group demography, based on findings that male–female interactions in baboons and other primates also depend on group composition (Archie et al., 2014; Bergman & Beehner, 2003; Rosenbaum, Maldonado-Chaparro, & Stoinski, 2016; Tung et al., 2012).

METHODS

Study Subjects

Study subjects were adult baboons from an intensively studied wild population inhabiting the Amboseli ecosystem of southern Kenya (Alberts, 2018; Alberts & Altmann, 2012). This population consists of multigeneration hybrids (Tung et al., 2008). Estimates from whole genome resequencing data indicate that while most baboons in Amboseli are predominantly yellow, admixture is pervasive (Vilgalys et al., 2021; Wall et al., 2016). Phenotypically, study subjects represent the full continuum, from animals that appear fully yellow to animals that are markedly anubis-like, with multiple representatives at all points along the continuum (Alberts & Altmann, 2001; Tung et al., 2008). This natural hybrid population is situated within a narrow hybrid zone that likely extends along the geographical boundary between yellow baboon and anubis baboon distributions in East Africa (Charpentier et al., 2012).

Members of the Amboseli baboon study population are individually recognized based on physical appearance and are monitored on a near-daily basis by trained observers who record demographic data (e.g. group membership, births, deaths, immigration, emigration) and behavioural data (e.g. social interactions, mating, travelling, resting, feeding). Importantly, the continuum of hybrid phenotypes has been present in Amboseli for many decades (Samuels & Altmann, 1986; Tung et al., 2008), meaning that anubis-like animals are not rare and/or unusually distinct to observers; our observational protocols, described below, also guard against nonrandom behavioural sampling. Study subjects were parous adult females (because parous females are strongly preferred over nulliparous females as mates by adult males of most primate species: Anderson, 1986; Gesquiere, Wango, Alberts, & Altmann, 2007) and adult males that had achieved a social dominance rank among other adult males in their group (Appendix, Table A1). Overall, we considered members of 12 social groups that were studied between November 1999 and December 2015. We restricted the data set to include only males and females for whom estimates of genetic ancestry, genetic diversity and genetic relatedness between individuals in male–female pairs could be calculated from previously generated microsatellite data (Buchan, Alberts, Silk, & Altmann, 2003; Tung et al., 2008, 2012). The resulting sample contained 136 females and 160 males, who together formed 3468 unique male–female dyads across the grooming and proximity data sets. These study subjects make up the vast majority of adult males (87%) and adult females (97%) in our population that otherwise met our inclusion criteria for this study (see Affiliative Social Behaviour below). Note that because we attempt to genotype every individual in our study groups, our genotyping protocol is unbiased with respect to ancestry.

Affiliative Social Behaviour

Grooming and maintenance of close spatial proximity (hereafter, proximity) are affiliative behaviours important to establishing, maintaining and strengthening social bonds in nonhuman primates (Cords, 1997, 2012; Palombit et al., 1997; Silk, Cheney, & Seyfarth, 2013). Although male–female grooming and proximity events were moderately correlated in our data set (Pearson's correlation: $r_{26,243} = 0.222$, $P < 10^{-15}$), we analysed grooming and proximity separately because grooming measures explained a small proportion of the variance in the proximity data (i.e. $r^2 = 0.049$). Almost all of the grooming data (99.8%) were collected during systematic monitoring of the population, following a sampling protocol in which observers move in a predetermined random order throughout the group. We refer to this data collection approach as 'representative interaction sampling'. In this sampling approach, observers record all grooming interactions in their line of sight, while simultaneously conducting random-order focal animal sampling on adult females. Therefore, observers rarely remain in the same location in the group for more than 10 min (the duration of each sample), which avoids biases due to uneven sampling of subjects. Additionally, members of baboon social groups in the Amboseli population are frequently spread out across a relatively large area, so there is no single central position in the group (Alberts, Archie, Altmann, & Tung, 2020; Archie et al., 2014). A potential concern with representative interaction sampling is that, because each observation day involves the same number of observers, regardless of group size, fewer grooming events per individual will inevitably be observed in larger groups. We control for this bias using a measure of observer effort (see Observer effort below). Additional grooming data, and all proximity data, were collected during random-order focal animal sampling on adult females, during which the identity of the nearest adult male within 5 m and grooming activity, if any, were recorded once per minute for the duration of each 10 min sample (Alberts et al., 2020).

For each co-resident opposite-sex dyad, we determined whether they were observed grooming or in proximity at least once during a given 2-month interval (see also Appendix, Additional Methods). We chose 2-month intervals as our unit for analysis to maximize comparability with an earlier analysis of ancestry effects on mating behaviour (Tung et al., 2012) and to facilitate unambiguous assignment of reproductive state to females (during longer intervals, females often switch between reproductive states, and in 2-month periods they do so as well but less frequently). We note that our 0/1 measure of grooming and proximity thus captures the probability that male–female affiliative behaviour occurs, and not the strength of a dyad's social bond. Specifically, even though bonds are formed via affiliative behaviour, accurate assessment of bond strength in this system generally requires ~1 year of observational data (Silk, Altmann, et al., 2006), a period that frequently overlaps multiple female reproductive states. We collected a mean ± SD of 63.3 ± 39.7 min (range 0–255) and 66.2 ± 37.5 min (range 8–255) of focal observation data per female per 2-month interval, for the grooming and proximity data sets, respectively.

We excluded data from periods in which behavioural monitoring was inconsistent or when social groups were too unstable (i.e. social groups were fissioning or fusing) to unambiguously

determine an individual's group membership. We also excluded all data from the 2009 hydrological year (1 November 2008–31 October 2009), which included the most severe drought documented in the Amboseli basin in more than 40 years (Okello et al., 2016; Tuqa et al., 2014). Omitting data from 2009 ensured that effects from this rare and extreme event, which altered patterns of female fertility and reproductive states, did not influence our results (Fitzpatrick, Altmann, & Alberts, 2014; Lea, Altmann, Alberts, & Tung, 2015).

Predictor Variables

We investigated the relationship between genetic ancestry and opposite-sex affiliative social behaviour using the following predictors, motivated in part by known predictors of mating behaviour in this population (Tung et al., 2012) (see Appendix, Table A2–A3 for correlations among all predictor variables).

Genetic ancestry

Genetic estimates of hybridity (i.e. the proportion of each individual's genome estimated to be from anubis ancestry) were included for females (h_f) and males (h_m). These estimates were based on genotypes at up to 13 highly polymorphic microsatellite markers and average ancestry assignments produced using the Bayesian clustering algorithm STRUCTURE 2.3.4 (Falush, Stephens, & Pritchard, 2003; Pritchard, Stephens, & Donnelly, 2000; see Tung et al., 2008; mean ± SD typed loci per individual = 12.40 ± 1.10). These assignments range continuously from 0 to 1, where 0 corresponds to unadmixed yellow baboon ancestry and 1 corresponds to unadmixed anubis baboon ancestry. These estimates are strongly correlated with recent genome-wide ancestry estimates (Pearson's correlation: $r_{21} = 0.717$, $N = 23$ individuals that overlapped between data sets, $P = 1.17 \times 10^{-4}$) (Wall et al., 2016); however, because genome-wide estimates are available for only a subset of the population, we used the microsatellite-based estimates here. Individuals in our study vary in their genetic ancestry from 0.03 to 0.92 (mean ± SD: 0.31 ± 0.28; see Appendix, Table A1 for genetic ancestry summary statistics, stratified by social group).

Assortative genetic ancestry index

To test the possibility that males and females of similar genetic ancestry are more likely to socially affiliate, we calculated a pairwise assortative genetic ancestry index, b, as a function of the genetic ancestry estimates of the female and male (h_f and h_m, respectively), paralleling the approach used in Tung et al.'s (2012) pairwise assortative mating index, a:

$$b = \max\left(h_m \times h_f, (1 - h_m) \times \left(1 - h_f\right)\right)$$

This index ranges from 0 to 1: high values indicate highly assortative male–female pairs (i.e. individuals in the pair both have low or high genetic ancestry estimates) and low values indicate highly disassortative male–female pairs (i.e. individuals in the pair have different genetic ancestry estimates). Intermediate values indicate male–female pairs where both individuals are of intermediate ancestry.

Heterozygosity

High genetic diversity is sometimes thought to be a measure of genetic quality (Kempenaers, 2007). Because it is relevant to mate choice (Kempenaers, 2007) and potentially social partner choice, we therefore included a measure of genetic diversity for both males and females using up to 14 highly polymorphic microsatellite markers (mean ± SD typed loci per individual = 13.13 ± 1.22; 13 of these markers were also used to assign genetic ancestry scores). We estimated individual genetic diversity by dividing the number of heterozygous loci by the number of genotyped loci for each individual (following Charpentier, Tung, Altmann, & Alberts, 2008). Importantly, there is no overall effect of species identity (i.e. yellow or anubis) on genetic diversity estimates using these markers (Charpentier et al., 2012). The correlation between genetic diversity and genetic ancestry is moderate within each sex (Pearson's correlation for both grooming and proximity: $r = 0.31$, $P < 10^{-4}$ for males; $r < 0.26$, $P < 0.01$ for females).

Relatedness

Because social affiliation may be affected by kinship, we included an estimate of genetic relatedness for each male–female dyad using the method of Queller and Goodnight (1989). These estimates, based on the same genotype data used to estimate heterozygosity, were calculated using the function 'coancestry' with the estimator 'quellergt' in the R package 'related' (v.1.0; Pew, Wang, Muir, & Frasier, 2015; Wang, 2011).

Social dominance rank

Social dominance rank can enhance access to valuable resources, including desirable social partners (e.g. Archie et al., 2014; Baniel et al., 2016; Haunhorst et al., 2019; Lemasson et al., 2008; Palombit et al., 2001). We therefore modelled female rank, male rank and the interaction between female and male ranks as additional fixed effects in the models. Female and male ranks were assigned separately for each sex, on a monthly basis, based on the outcomes of dyadic agonisms between all pairs of individuals in the same group (Alberts et al., 2020; Alberts & Gordon, 2018). We represented rank using an ordinal approach, where the highest-ranking individual holds rank 1 and lower-ranking individuals occupy ranks of successively higher numbers. Since female and male ranks were assigned on a monthly basis and our time window for analyses of grooming and proximity interactions spanned a 2-month period, we used the average of each individual's rank across both months for each 2-month interval. Note that although higher-ranking males and anubis-like males are more likely to gain consortships in this population (Tung et al., 2012), genetic ancestry is not correlated with dominance rank ($P > 0.35$ for both grooming and proximity data sets; see also Franz, McLean, Tung, Altmann, & Alberts, 2015).

Age

Female age may also affect a female's social interactions. To account for possible age-related effects, we modelled a linear effect of female age, averaged across each 2-month analysis window (i.e. her age at the start of the second month), as a continuous predictor variable in our models. We also included a transformed measure of female age that reflects the relationship between female age and conception probability in this population, where the highest conception probability occurs at ~14 years of age (Beehner, Onderdonk, Alberts, & Altmann, 2006). Following Tung et al. (2012), we calculated female-transformed age, a_t, as a function of a_u, the untransformed female age:

$$a_t = -1 \times \left(\frac{a_u - 14}{14}\right)^2$$

This transformation assigns 0 for the value of a_t at 14 years, the age at which conception probabilities are highest; values of a_t

become increasingly negative with distance from age 14. For 90.4% (123 out of 136) of the females in the data set, birth dates were known to within a few days. For the other females in the data set, birth dates were estimated to within 6 months (i.e. ±3 months' error). Male age was not included in any models since it is tightly correlated with rank in male baboons (Alberts, Watts, & Altmann, 2003) and its effect on mating and social behaviour is likely to be linked to rank (Silk et al., 2020; Tung et al., 2012).

Group composition

To incorporate group level demographic effects on social behaviour, we included the number of adult females and the number of adult males in the social group of a male–female pair in both models (averaged across each 2-month analysis period).

Reproductive state

Because female reproductive state affects the stability of male–female bonds in other baboon species (Baniel et al., 2016; Weingrill, 2000), we also included female reproductive state as a categorical variable in our models. To capture opposite-sex affiliation outside the context of mating, we excluded all data points in which the female member of a potential pair was cycling. Thus, reproductive state was either pregnant or lactating, both of which meant that the female was not actively mating and could not conceive. Pregnancy and lactation were coded as -1 and 1, respectively, which avoided numerical instability that occurred if we used a 0/1 encoding (see Appendix, Additional Methods). To test whether the effects of female reproductive state on male–female social affiliation depended on genetic ancestry, we also modelled an interaction between female reproductive state and female genetic ancestry and a separate interaction between female reproductive state and male genetic ancestry.

Pair co-residency

The number of days that a male and female were observed in the same social group may influence both their tendency to affiliate and our ability to detect interactions between them. We therefore included the total number of days in each 2-month interval that a male and female were censused in the same group as a model covariate.

Observer effort

The number of field observers and the amount of time spent conducting behavioural observations for each study group was consistent across all study groups regardless of their size (Appendix, Fig. A1). Consequently, the probability of observing grooming or proximity events could vary as a function of social group size, because an observer watching a small group is likely to capture a larger fraction of interactions in a given period than that same observer watching a much larger group (note that had we measured the 'proportion of time' a dyad was in proximity – conditional on the female being observed – instead of as a binary event, observer effort would not be expected to affect the outcome). Thus, we calculated observer effort and included it as a covariate in both models. Observer effort was estimated as the average number of minutes of focal sample data collected per adult female per social group in a given 2-month interval (see Appendix, Additional Methods).

Statistical Analyses

Grooming and proximity behaviour were modelled as binary events and analysed separately using binomial mixed effects models. Each row of data corresponded to a unique, co-resident female–male dyad in a given 2-month interval and was assigned a value of '1' if the dyad was observed grooming or in proximity at least once during the 2-month interval and a '0' if they were not. We used 2 months as our time interval because our resolution for grooming and proximity behaviour is relatively coarse on a month-to-month basis, even after excluding months in which observer effort was low (see Appendix, Additional Methods).

We retained all 2-month intervals in which focal females groomed or were in proximity with any candidate male social partner at least once, except for 2-month intervals in which females transitioned between reproductive states and 2-month intervals in which the average number of adult males in the social group was less than two. We also excluded any male in a female's 2-month interval if he was only present for 1 of the 2 months and excluded all data for females and males who were observed for less than 8 months because sparse data makes it difficult to estimate individual level random effects. The final grooming data set included 127 unique females and 160 unique males across 1866 female 2-month intervals (17 356 total female–male pair–interval combinations), and the final proximity data set included 131 unique females and 160 unique males across 2338 female 2-month intervals (21 130 total female–male pair–interval combinations).

We ran binomial mixed effects models using the function 'glmmTMB' (family = 'binomial') in the R package 'glmmTMB' (v.1.0.0; Brooks et al., 2017), using a logit link:

$$y_{ij} \sim Bin\left(1, p_{ij}\right)$$

$$p_{ij} = \text{logit}(\beta_0 + \boldsymbol{X_{ij}}\boldsymbol{\beta} + m_i + f_i + \varepsilon_{ij})$$

where y_{ij} is a 0/1 value indicating whether male–female dyad i was observed grooming or in proximity during a 2-month interval j. y_{ij} is drawn from a binomial distribution, where the probability of grooming or proximity (p_{ij}) is modelled as the function of the logit-transformed sum of (1) the intercept, β_0; (2) the fixed effects ($\boldsymbol{X_{ij}}\ \boldsymbol{\beta}$) of male genetic ancestry, female genetic ancestry, the assortative genetic ancestry index for that pair, male heterozygosity, female heterozygosity, genetic relatedness between individuals in that pair, male dominance rank, female dominance rank, female age, transformed female age, the number of adult females in the social group, the number of adult males in the social group, female reproductive state (pregnant or lactating), the interaction between female reproductive state and female genetic ancestry, the interaction between female reproductive state and male genetic ancestry, the interaction between male and female dominance ranks, pair co-residency and observer effort ($\boldsymbol{X_{ij}}$ represents all of these data using standard matrix notation and $\boldsymbol{\beta}$ refers to the vector of all fixed effect estimates); and (3) the random effects of male identity, m_i, and female identity, f_i. ε_{ij} represents model error.

To assess statistical significance, we used permutation tests to account for unequal representation of individuals in the data set and predictors that did not follow standard parametric distributions. We followed the procedure of Tung et al. (2012), who conducted a similar analysis on mating behaviour. Specifically, we first computed, for each female–interval combination, the proportion of dyads where an event (grooming or proximity) occurred. These

values are estimates of the probability of grooming or proximity with any male, per female–interval combination. These probabilities were then permuted across all female 2-month intervals, and randomized response variables (0/1) were generated by drawing from a binomial distribution with p_{ij} equal to the permuted grooming or proximity probability for each female–interval. This approach preserves the structure of the predictor variables (including correlations between predictors), the number of times each individual is represented in the data set and the distribution of grooming or proximity events for each female–interval. We then fitted the model used to analyse the real data to the permuted data set and calculated a *P* value for each predictor variable based on the number of times that the absolute value of the effect size estimated from the permuted data sets was greater than the absolute value of the effect size estimated from the observed data set, across 1000 permutations. All analyses were run in R (v.3.6.1; R Core Team, 2019).

Ethical Note

The research in this study was approved by the Institutional Animal Care and Use Committee (IACUC) at Duke University (no. A273-17-12) and adhered to the laws and guidelines of the Kenyan government. The majority of our data collection was entirely noninvasive. The animals are completely habituated to the presence of observers and show no signs of stress associated with observation. Observers further reduce animal stress by maintaining at least a 5 m distance from habituated study subjects during observational sampling, and faecal samples for genotyping were not collected until all animals moved away from where the sample was deposited. The animals experience no stress during faecal sample collection. For the minority of samples for which microsatellite genotypes were obtained from blood, samples were collected using a minimally invasive protocol on animals that had been briefly anaesthetized (Lea et al., 2018; Sapolsky & Altmann, 1991; Tung et al., 2011). Stress is reduced by darting only when animals are not looking towards the observer, by keeping the period of anaesthetization brief (usually less than 1 h), by ensuring that the animals are kept in a quiet, undisturbed area in the shade during recovery and by returning them to their social groups as quickly as possible (usually within 4 h of anaesthetization). The darting protocol is overseen by a veterinarian and includes animal welfare oversight. In all cases, study subjects returned quickly to their social group and showed no signs of adverse reactions to the sampling.

RESULTS

Individual Characteristics: Genetic Ancestry and Dominance Rank Predict Opposite-sex Affiliative Social Behaviour in Males and Females

Our models identified two male characteristics that consistently predicted opposite-sex grooming and proximity behaviour (Tables 1–2). Specifically, grooming and proximity were more likely to occur if the male in the dyad had more anubis ancestry (grooming: $\beta = 0.429$, $P < 0.001$; Table 1, Fig. 1a; proximity: $\beta = 0.270$, $P < 0.001$; Table 2, Appendix, Fig. A2a) and was higher ranking (grooming: $\beta = -0.096$, $P < 0.001$; Table 1, Fig. 1b; proximity: $\beta = -0.047$, $P < 0.001$; Table 2, Appendix, Fig. A2b). Male heterozygosity was not significantly associated with either grooming or proximity behaviour.

Similar patterns were observed for females, although the effect of female rank was weaker than that of male rank. Grooming and proximity were more likely to occur if the female in a dyad had more anubis ancestry (grooming: $\beta = 0.513$, $P < 0.001$; Table 1, Fig. 1c; proximity: $\beta = 0.270$, $P = 0.022$; Table 2, Appendix, Fig. A2c) and was higher ranking (grooming: $\beta = -0.027$, $P < 0.001$; Table 1, Fig. 1d; proximity: $\beta = -0.024$, $P < 0.001$; Table 2, Fig. A2d). Female reproductive state, female age, transformed female age and female heterozygosity did not significantly affect grooming or proximity behaviour, nor did the interaction between female reproductive state and female genetic ancestry.

Dyad Level Characteristics: Traits of Both Partners Predict the Propensity to Affiliate with the Opposite Sex

In addition to individual level effects, we found that the combined characteristics of the female and male in each dyad predicted the probability of grooming and proximity. First, affiliative

Table 1
Results from a multivariate logistic regression model predicting grooming behaviour

	Predictor variable[a]	Effect estimate	*P*[b]	Effect direction[c]
Intercept		−1.474	0.339	–
Genetic effects	**Female genetic ancestry**	**0.513**	**<0.001**	**More anubis ancestry in females → ↑ Pr(groom)**
	Male genetic ancestry	**0.429**	**<0.001**	**More anubis ancestry in males → ↑ Pr(groom)**
	Assortative genetic ancestry index (*b*)	**0.646**	**<0.001**	**Females and males of similar genetic ancestry → ↑ Pr(groom)**
	Female heterozygosity	−0.249	0.406	–
	Male heterozygosity	0.228	0.189	–
	Genetic relatedness	−0.090	0.489	–
Rank effects	**Female ordinal rank**	**−0.027**	**<0.001**	**Higher ranking females → ↑ Pr(groom)**
	Male ordinal rank	**−0.096**	**<0.001**	**Higher ranking males → ↑ Pr(groom)**
	Female ordinal rank × male ordinal rank	**0.003**	**<0.001**	**Females and males of similar rank → ↑ Pr(groom)**
Age effects	Female age (a_u)	−0.007	0.332	–
	Female age transformed (a_t)	−0.192	0.562	–
Demographic effects	**Adult females in group**	**−0.039**	**<0.001**	**More adult females in group → ↓ Pr(groom)**
	Adult males in group	*−0.030*	*0.018*	*More adult males in group → ↓ Pr(groom)*
Reproductive state effects	Reproductive state (pregnant = −1, lactating = +1)	−0.067	0.165	–
	Reproductive state (as above) × female genetic ancestry	0.086	0.412	–
	Reproductive state (as above) × male genetic ancestry	0.004	0.949	–
Co-residency effects	**Pair co-residency**	**0.047**	**<0.001**	**Longer co-residency → ↑ Pr(groom)**
Observer effects	Observer effort	0.002	0.425	–

[a] All variables included in this table were fitted as fixed effects in the multivariate logistic regression model. Male and female identity were fitted as random effects.
[b] Predictor variables for which $P < 0.01$ are bolded and $0.01 < P < 0.05$ are italicized.
[c] Pr(groom) = probability of observing grooming between a given male–female dyad at least once during a 2-month interval.

Table 2
Results from a multivariate logistic regression model predicting proximity behaviour

	Predictor variable[a]	Effect estimate	P[b]	Effect direction[c]
Intercept		−1.584	0.008	–
Genetic effects	*Female genetic ancestry*	*0.270*	*0.022*	*More anubis ancestry in females → ↑ Pr(prox)*
	Male genetic ancestry	**0.270**	**<0.001**	**More anubis ancestry in males → ↑ Pr(prox)**
	Assortative genetic ancestry index (b)	**0.303**	**<0.001**	**Females and males of similar genetic ancestry → ↑ Pr(prox)**
	Female heterozygosity	−0.120	0.654	–
	Male heterozygosity	0.042	0.745	–
	Genetic relatedness	−0.041	0.693	–
Rank effects	**Female ordinal rank**	**−0.024**	**<0.001**	**Higher ranking females → ↑ Pr(prox)**
	Male ordinal rank	**−0.047**	**<0.001**	**Higher ranking males → ↑ Pr(prox)**
	Female ordinal rank × male ordinal rank	*0.001*	*0.011*	*Females and males of similar rank → ↑ Pr(prox)*
Age effects	Female age (a_u)	−0.004	0.644	–
	Female age transformed (a_t)	−0.028	0.916	–
Demographic effects	Adult females in group	−0.018	0.073	–
	Adult males in group	**−0.036**	**0.005**	**More adult males in group → ↓ Pr(prox)**
Reproductive state effects	Reproductive state (pregnant = −1, lactating = +1)	0.056	0.187	–
	Reproductive state (as above) × female genetic ancestry	0.021	0.851	–
	Reproductive state (as above) × male genetic ancestry	−0.059	0.269	–
Co-residency effects	**Pair co-residency**	**0.037**	**<0.001**	**Longer co-residency → ↑ Pr(prox)**
Observer effects	**Observer effort**	**0.027**	**<0.001**	**Greater observer effort → ↑ Pr(prox)**

[a] All variables included in this table were fitted as fixed effects in the multivariate logistic regression model. Male and female identity were fitted as random effects.
[b] Predictor variables for which $P < 0.01$ are bolded and $0.01 < P < 0.05$ are italicized.
[c] Pr(prox) = probability of observing a given male–female dyad in proximity at least once during a 2-month interval.

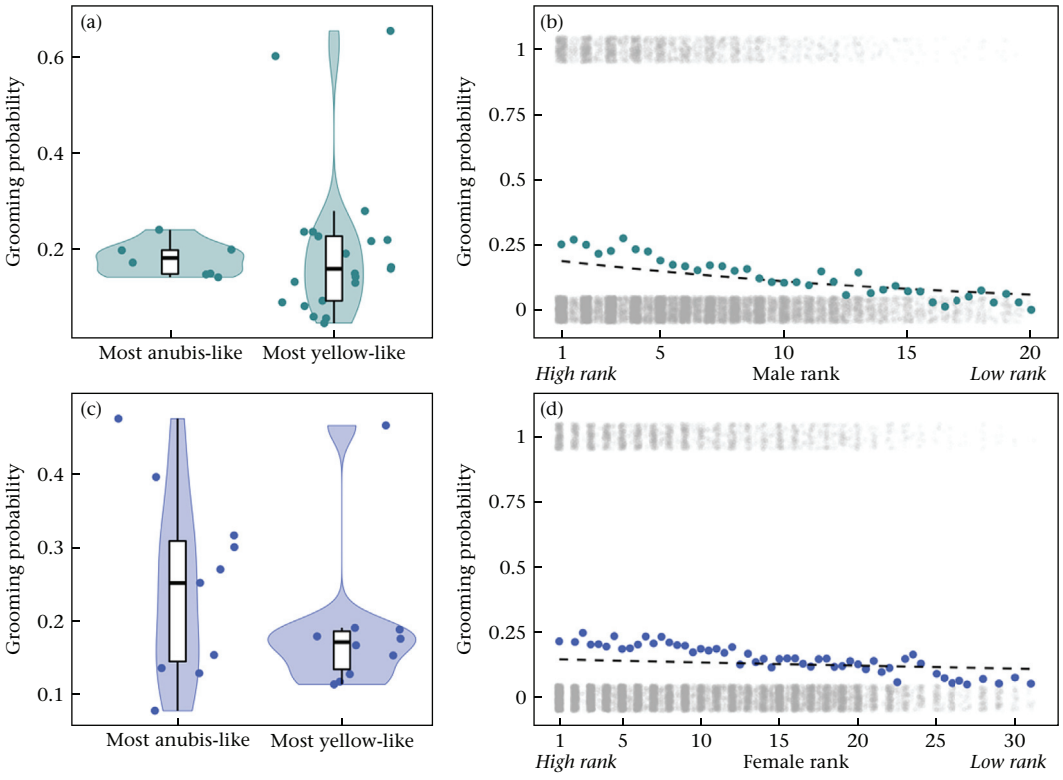

Figure 1. The influence of genetic ancestry and dominance rank on the tendency to groom with an opposite-sex partner. (a) The probability of grooming among co-resident opposite-sex pairs, per 2-month interval, for the most anubis-like males (above the 90th percentile for male genetic ancestry in the data set, >83.6% anubis ancestry, $N = 8$ males) and the most yellow-like males (below the 10th percentile for male genetic ancestry in the data set, <4.8% anubis ancestry, $N = 21$ males). Probabilities are shown here based on the data without adjustment for other covariates. (b) The probability of grooming among co-resident opposite-sex pairs, per 2-month interval, as a function of male dominance rank. Coloured dots show probabilities based on counts of grooming occurrences, without adjustment for other covariates (as in (a)), and the dashed line shows the predicted relationship based on model estimates, assuming average values for all other covariates (see Appendix, Additional Methods). Grey dots show the presence ($y = 1$) or absence ($y = 0$) of grooming behaviour for all 17 356 female–male pair–interval combinations, as a function of male dominance rank (dots are jittered vertically for visibility). Noninteger values correspond to individuals that changed ranks during a 2-month interval in the data set. (c) As in (a), for the most anubis-like females (above the 90th percentile for female genetic ancestry in the data set, >76.0% anubis ancestry, $N = 11$ females) and the most yellow-like females (below the 10th percentile for female genetic ancestry in the data set, <3.5% anubis ancestry, $N = 10$ females). (d) As in (b), with the probability of grooming shown as a function of female dominance rank.

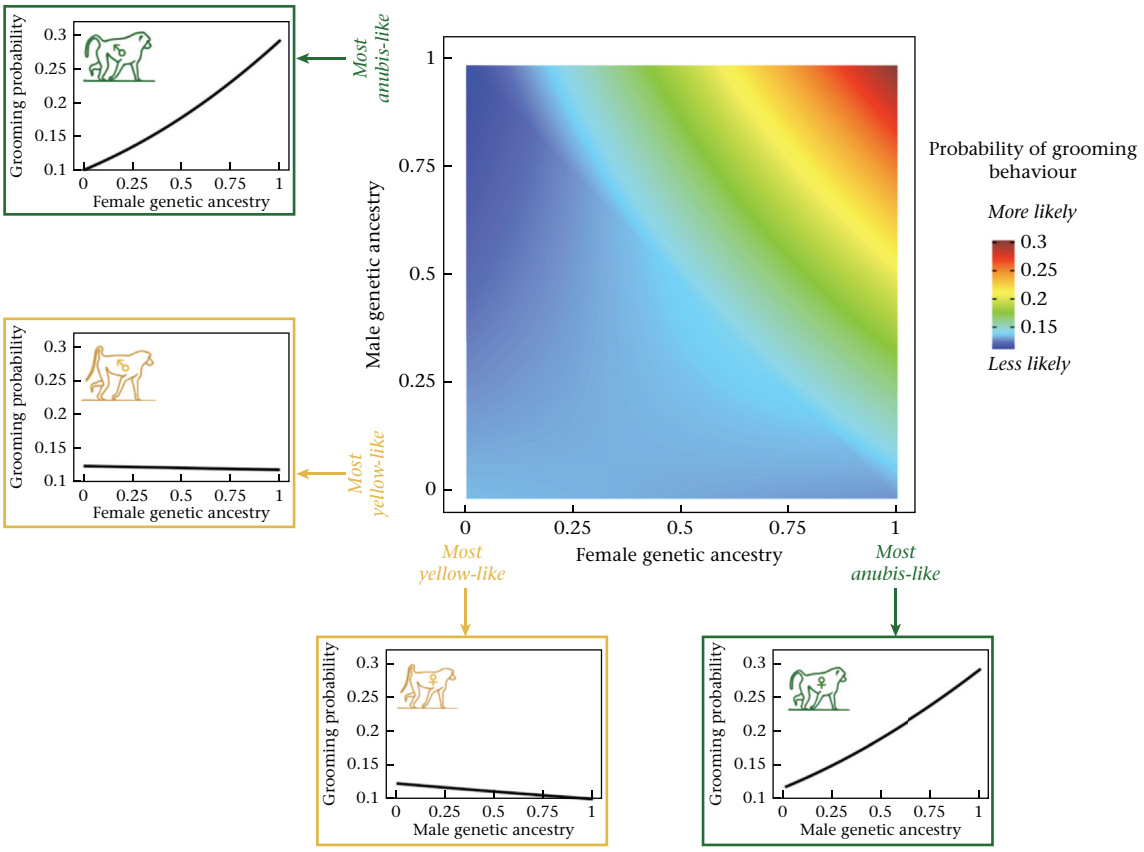

Figure 2. The combined effect of genetic ancestry characteristics of females and males on the probability of grooming. The central heatmap shows the probability of grooming behaviour as a function of female genetic ancestry (*X* axis) and male genetic ancestry (*Y* axis), based on model estimates assuming average values for all other covariates (see Appendix, Additional Methods). Assortative affiliative behaviour is reflected by the increased probability of yellow-like females grooming with yellow-like males, relative to anubis-like males, and anubis-like females grooming with anubis-like males, relative to yellow-like males. The probability of grooming is highest for pairs where both partners are anubis-like. Line graphs surrounding the heatmap show model predictions for the probability of grooming behaviour for males (left) and females (bottom) at the two extremes of genetic ancestry, as a function of the genetic ancestry of potential opposite-sex social partners.

interactions were assortative with respect to genetic ancestry: they were more likely to occur when both partners were of similar genetic ancestry (i.e. both anubis-like or both yellow-like) and less likely to occur if they were of different genetic ancestry (grooming: $\beta = 0.646$, $P < 0.001$; Table 1, Fig. 2; proximity: $\beta = 0.303$, $P < 0.001$; Table 2, Appendix, Fig. A3). Overall, the probability of grooming and proximity was highest for pairs where both partners were anubis-like. Affiliative interactions were also assortative with respect to dominance rank: if both partners were high ranking, the probability of affiliative interaction was higher than explained by the separate, additive effects of high male rank and high female rank alone (grooming: $\beta = 0.003$, $P < 0.001$; Table 1, Fig. 3; proximity: $\beta = 0.001$, $P = 0.011$; Table 2, Appendix, Fig. A4). The effects of ancestry-based assortativity and rank-based assortativity are likely to be independent, as the assortative genetic ancestry index we used here was only weakly correlated with the product of male and female rank (absolute value of Pearson's correlation: $r < 0.07$, $P < 3.7 \times 10^{-13}$ for both grooming and proximity data sets). The correlation between rank and genetic ancestry was similarly weak within each sex (absolute value of Pearson's correlation: $r < 0.03$ for unique male rank–genetic ancestry combinations, $P > 0.35$ for both grooming and proximity; $r < 0.08$ for unique female rank–genetic ancestry combinations, $P = 0.37$ for grooming and $P = 0.04$ for proximity).

Genetic relatedness did not predict either grooming or proximity behaviour within dyads (grooming: Table 1; proximity: Table 2), in contrast to the effects of relatedness on mating behaviour, where relatives are less likely to mate (consistent with inbreeding avoidance in baboons: Alberts & Altmann, 1995; Packer, 1979a; Tung et al., 2012). In other words, opposite-sex kin were neither more likely nor less likely to socially affiliate than opposite-sex nonkin. Additionally, male–female affiliation did not depend on the interaction between female reproductive state and male genetic ancestry (grooming: Table 1; proximity: Table 2).

Group Demography Influences Grooming and Proximity Behaviour, and Observer Effort Affects Ascertainment of These Behaviours

In addition to individual and dyad level effects, we found that aspects of group demography also influence male–female affiliative behaviour. The probability of grooming was lower for all dyads when the social group contained more adult males ($\beta = -0.030$, $P = 0.018$; Table 1, Appendix, Fig. A5a–b) and more adult females ($\beta = -0.039$, $P < 0.001$; Table 1, Appendix, Fig. A6a–b). Similarly, the probability of proximity was lower for all dyads when the social group contained more adult males ($\beta = -0.036$, $P = 0.005$; Table 2, Appendix, Fig. A5c–d), but not more adult females ($\beta = -0.018$, $P = 0.073$; Table 2, Appendix, Fig. A6c–d).

Finally, the probability of grooming and proximity behaviour was higher for all dyads the more days they were observed together in the same group (grooming: $\beta = 0.047$, $P < 0.001$; Table 1; proximity: $\beta = 0.037$, $P < 0.001$; Table 2). The probability of observing a given male–female dyad in proximity, but not of observing them

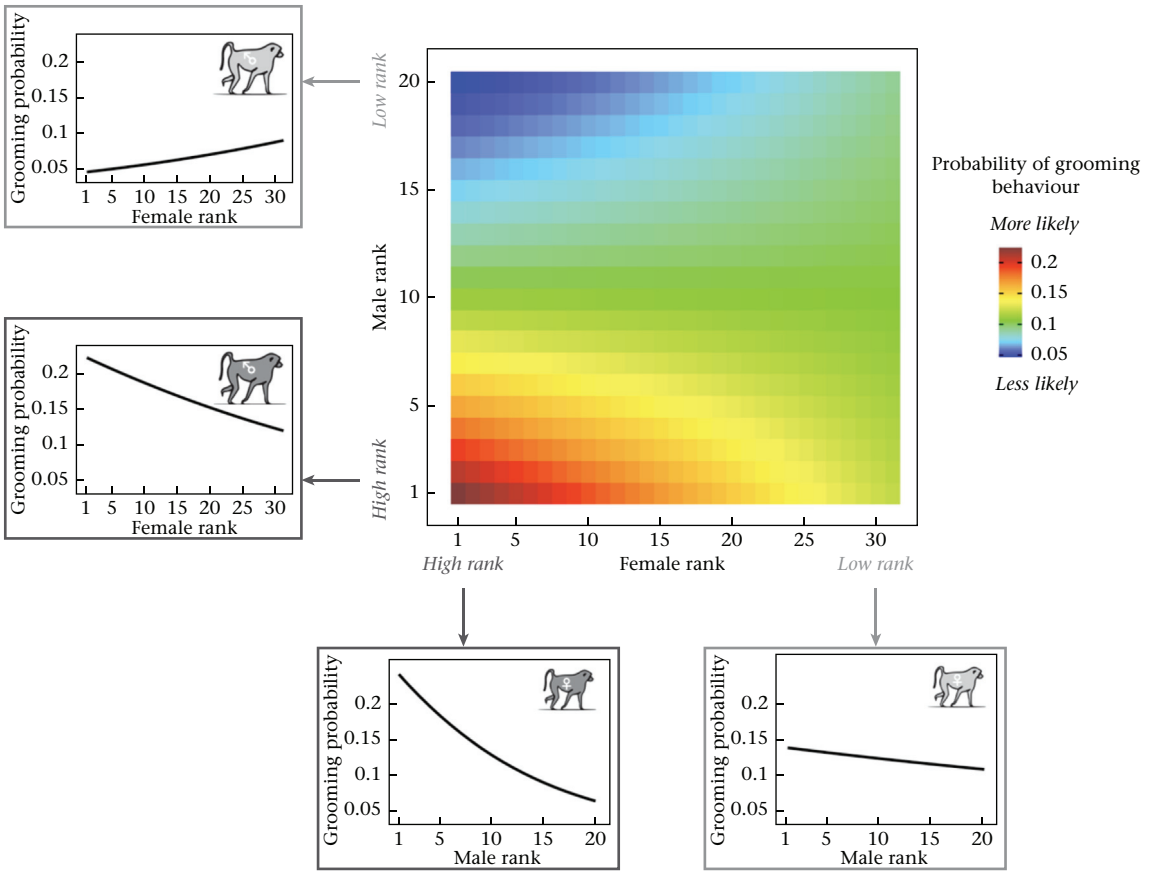

Figure 3. The combined effect of rank characteristics of females and males on the probability of grooming. The central heatmap shows the probability of grooming behaviour as a function of female dominance rank (*X* axis) and male dominance rank (*Y* axis), based on model estimates assuming average values for all other covariates (see Appendix, Additional Methods). The probability of grooming is highest for pairs where both partners are high ranking. Line graphs surrounding the heatmap show model predictions for the probability of grooming behaviour for males (left) and females (bottom) at the extremes of the rank distribution, as a function of the dominance rank of potential opposite-sex social partners.

grooming at least once, also increased with greater observer effort (grooming: $\beta = 0.002$, $P = 0.425$; Table 1; proximity: $\beta = 0.027$, $P < 0.001$; Table 2).

DISCUSSION

Our results show that opposite-sex affiliative relationships are predicted by genetic ancestry in a natural baboon hybrid zone. Genetic ancestry effects are of particular interest because opposite-sex relationships must have a partial genetic basis in order to respond to natural selection. Additionally, genetic ancestry-associated differences provide prima facie evidence that this trait has evolved in the past. Specifically, in the Amboseli baboons, genetic ancestry acts alongside the effects of dominance rank and group demography to predict grooming and proximity behaviour between adult males and adult females outside the mating context. These effects are not only detectable as a function of the individual characteristics of males and females, but also as a function of the properties of each opposite-sex pair. Although more anubis-like males and females were more likely to affiliate with the opposite sex regardless of their partner's ancestry, pairs of anubis-like males and anubis-like females were the most likely to be observed grooming or in close proximity (Fig. 2, Appendix, Fig. A3). Our findings thus suggest that the tendency to engage in opposite-sex affiliative behaviour partially diverged during baboon evolution to differentiate yellow and anubis baboons. We note that while we tested for the effects of genetic ancestry in this study, not genotype per se, baboons in Amboseli inherit anubis ancestry from both maternal and paternal lines (Tung et al., 2008). Our data set also contains many multigeneration hybrids, such that genetic ancestry estimates vary continuously between mostly yellow to mostly anubis. Thus, the signature of genetic ancestry reported here likely arises from ancestry-associated differences in genotype, as opposed to ancestry-associated maternal or environmental effects on social preference.

These results add to previous evidence that male–female social bonds vary across baboon species (Baniel et al., 2016; Fischer et al., 2017; Goffe et al., 2016; Nguyen et al., 2009; Städele et al., 2019; Weingrill, 2000). For instance, male–female social relationships in chacma baboons, *Papio ursinus*, are short-lived and occur primarily when females have dependent infants, whereas in Guinea baboons, *Papio papio*, close male–female social relationships commonly last for several years (Baniel et al., 2016; Fischer et al., 2017; Goffe et al., 2016). Yellow and anubis baboons, which have similar social organization and mating systems (multimale, multifemale groups with male-biased dispersal and polygynandry), are thought to fall between these two extremes, such that male–female relationships can sometimes, although not always, be long-lasting (Nguyen et al., 2009; Smuts, 1985; Städele et al., 2019). The identification of genetic ancestry effects in this study thus suggests that subtle differences in the nature of opposite-sex social relationships can evolve even between species that are otherwise quite similar in their social systems and behavioural repertoires.

Our results also support an emerging perspective that behavioural variation within the genus *Papio* is relatively continuous (Fischer, Higham, et al., 2019). If so, the commonly used distinction

between multilevel societies (e.g. as in Guinea and hamadryas baboons) and single level societies (e.g. as in yellow, anubis, chacma and Kinda baboons, *Papio kindae*) is not sufficient to capture behavioural diversity in baboons. Our finding that anubis-like individuals more readily affiliate with opposite-sex social partners than yellow-like individuals also suggests that anubis baboons share behavioural similarities with other 'northern clade' baboons (Guinea and hamadryas) that may reflect their shared genetic history (Jolly, 2020; Rogers et al., 2019). Interestingly, while more anubis-like baboons in our study were relatively more social with the opposite sex compared to yellow-like baboons, anubis baboons are comparably less social with opposite-sex partners than hamadryas baboons in the anubis–hamadryas Ethiopian hybrid zone (Bergman & Beehner, 2004). This again highlights that both substantial, discrete differences (e.g. between Guinea baboons and chacma baboons) and subtle, continuous variation (e.g. between the yellow baboons and anubis baboons in our study) characterize social behaviour in the baboon genus (Fischer, Higham, et al., 2019).

Several lines of evidence also support the relevance of genetic ancestry effects on opposite-sex affiliative behaviour to current variation in fitness. First, opposite-sex social relationships predict longevity in the Amboseli baboons (Archie et al., 2014; Campos et al., 2020), and longevity is an important contributor to lifetime reproductive success in both male and female baboons, as well as in other long-lived vertebrates (Alberts, Buchan, & Altmann, 2006; Clutton-Brock, 1988; Lawler, 2007; McDonald, 1993; McLean, Archie, & Alberts, 2019; Newton, 1989; Wroblewski et al., 2009). Second, male–female social bonds can also lead to other reproductive gains, including offspring care that may improve survival (Anderson, 1992; Buchan et al., 2003; Busse & Hamilton, 1981; Huchard et al., 2013; Moscovice et al., 2009; Nguyen et al., 2009; Silk et al., 2020). Indeed, our findings that affiliative behaviour was less common for any given dyad in large groups and that both male and female rank predicted social interactions suggest that male–female social bonds are an important and limited social resource for both sexes (Archie et al., 2014; Baniel et al., 2016; Haunhorst et al., 2019; Lemasson et al., 2008; Palombit et al., 2001; Seyfarth, 1976; Städele et al., 2019). This interpretation agrees with reports in chacma baboons that pregnant and lactating females direct aggression towards cycling females that are mate-guarded by and copulate with a shared male social partner (Baniel et al., 2018). Together with ancestry-related differences in affiliative behaviour, our observations indicate that opposite-sex affiliative behaviour has not only evolved in baboons in the past, but may also be the target of selection in the Amboseli population today.

The long-term ramifications of our findings for the stability or resolution of the hybrid zone remain somewhat unclear. If strong opposite-sex social bonds are fitness enhancing, more anubis-like ancestry should be favoured in Amboseli. However, assortative social preferences (both in mating and nonmating contexts) can also act as a barrier to admixture and could reduce the rate of anubis expansion. Along with previous findings in Amboseli (Charpentier et al., 2008; Franz et al., 2015; Tung et al., 2012), our results thus suggest that genetic ancestry is associated with a range of selectively relevant behavioural and life-history traits that do not universally point towards either anubis range expansion or to behaviourally mediated reproductive isolation. Furthermore, any effect of genetic ancestry in baboons must necessarily be filtered through the effect of dominance rank, which is the most robust predictor of male mating behaviour and, based on the results of this study, also a major contributor to opposite-sex affiliative behaviour (Tung et al., 2012). Finally, the effect of assortativity necessarily depends on the characteristics of available social partners. The interplay between genetic ancestry effects on an individual level and at the dyadic level will therefore be dynamic across populations and over time. The complexity of these co-acting factors may help explain why yellow baboons and anubis baboons remain phenotypically and genetically distinct, even though genomic analyses indicate repeated bouts of gene flow between yellow baboons and anubis baboons over hundreds to thousands of generations (Rogers et al., 2019; Wall et al., 2016). More broadly, our results suggest that simple behavioural barriers to admixture, such as wing pattern-based mate choice in butterflies or vibrational-based courtship signals in treehoppers (Jiggins, Naisbit, Coe, & Mallet, 2001; Rodríguez, Sullivan, & Cocroft, 2004), are unlikely to occur in socially complex animals like baboons. Future work using social network analysis, which could help reveal how genetic ancestry structures the topology and connectivity of social relationships in whole groups, may help shed light on this question.

Finally, our study suggests both parallels and differences between opposite-sex social interactions within versus outside the context of mating. Specifically, effects of female age and kinship were weak or undetectable in our analysis of male–female affiliative behaviour outside the mating context. These results contrast with our previous results for mating: male baboons are less likely to mate with females in older age classes (Tung et al., 2012), and baboons and other primates avoid mating with relatives (Alberts & Altmann, 1995; Godoy, Vigilant, & Perry, 2016; Packer, 1979a; Tung et al., 2012; Walker et al., 2017; Widdig et al., 2017), probably as a behavioural strategy that minimizes inbreeding depression (Robinson et al., 2019). However, in both settings, higher-ranking and more anubis-like males are more likely to interact with females, and assortativity by genetic ancestry and dominance rank characterizes both mating and male–female affiliative behaviour (Tung et al., 2012). These parallels could be partially explained if mating success also leads males to affiliate with the mothers of their joint offspring, after those offspring are born. If so, anubis-like males who are successful at gaining consortships would also be involved in more female-directed affiliative behaviour. Indeed, evidence from several studies of baboons suggests that males frequently form affiliative relationships with the mothers of their genetic offspring (Huchard et al., 2010; Moscovice et al., 2010; Nguyen et al., 2009; Silk et al., 2020; Städele et al., 2019). In contrast, opposite-sex social affiliation is not a strong predictor of future mating events (Huchard et al., 2010; Moscovice et al., 2010; Nguyen et al., 2009; Silk et al., 2020; Städele et al., 2019), so differences in male–female behaviour in mating versus nonmating contexts may arise because the benefits of opposite-sex social bonds differ from the benefits of mating. Female choice and female–female competition may also be more important in predicting grooming and proximity than mating behaviour. For instance, whereas only one or a few females experience oestrus at any given time (Bercovitch, 1983; Bulger, 1993; Levy et al., 2020), all adult females are available as, and may actively be searching out, grooming partners. Notably, grooming relationships in baboons are more often initiated and maintained by females than by males, whereas males primarily bear the costs of mate guarding in a mating context (Alberts, Altmann, & Wilson, 1996; Nguyen et al., 2009; Packer, 1979b; Palombit et al., 1997; but see Weyher, Phillips-Conroy, Fourrier, & Jolly, 2014). Thus, sexual and social preferences, and the extent to which they are expressed by males versus females, are likely to vary across different types of opposite-sex relationships – a distinction reminiscent of differences between social monogamy and genetic monogamy in pair-bonded birds and mammals (Carter & Perkeybile, 2018; Gowaty, 1996).

Data Availability

Data on grooming behaviour and proximity behaviour and all predictor variables tested in our models are available in the Duke

Research Data Repository at https://doi.org/10.7924/r4kp82d1z. R code for recreating the analyses and figures in the manuscript is available at https://github.com/ArielleF/Genetic-Ancestry-Social-Affiliation.

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Appendix

Additional Methods

Estimating observer effort

All baboon study groups are observed by the same number of field observers for roughly the same amount of time, regardless of group size. As a consequence, the individual level density of our grooming and proximity data varies by social group (i.e. there are differences among groups in observer effort per individual baboon). To account for these differences, we estimated observer effort using focal animal sampling data from adult females. Each focal sample typically consists of 10 point samples, collected once per minute, for 10 min (Alberts et al., 2020; Archie et al., 2014). We summed the total number of point samples collected for adult females per social group across each female's 2-month interval and then divided this value by the total number of adult females present in the social group during that same time period. We used this value as a measure of observer effort and included it as a fixed effect covariate in our models.

Filtering of grooming and proximity data

In the main text, we report results for grooming and proximity behaviour using 2-month time intervals. Initially, we attempted to measure grooming and proximity behaviour on a monthly basis. However, on a monthly basis, grooming and proximity were not observed in 93.2% and 87.2% of rows ($N = 62\,195$ total rows, where a row represents a male–female dyad that could potentially be observed grooming or in proximity), respectively. While some of these '0' value rows reflect a true absence of male–female interactions, observations in a single month may be too sparse to accurately reflect whether a given male–female dyad interacted. Indeed, even after omitting social group-month combinations with low observer effort (i.e. less than an average of 20 point samples per female per social group-month), grooming and proximity were still not observed in 92.1% and 83.9% of the data set, respectively. Thus, we concluded that our resolution of grooming and proximity behaviour was too coarse to measure on a monthly basis.

To address this concern, we expanded our time window from one month to two months and excluded any male in a female's 2-month interval if he was only present for one of the two months. This decision reduced the percentage of rows where grooming and proximity did not occur (87.9% and 76.9% of rows, respectively, $N = 26\,245$ total rows). Because we were most interested in the predictors of opposite-sex affiliative behaviour, conditioned on it actually occurring, we also filtered out any 2-month interval where the focal female did not interact with any male social partner for the entire interval (31.7% and 17.1% of intervals for the grooming and proximity data sets, respectively). We performed this filtering separately for the grooming and proximity data sets, thus producing two separate data sets for downstream analysis. We also excluded all data for females and males who were observed for less than 8 months. If these filters resulted in no observations of grooming or proximity for a given female interval, we also removed that interval (and repeated this procedure until all filtering criteria were met). Finally, we did not consider 2-month intervals in which females transitioned between reproductive states (pregnant or lactating) and 2-month intervals in which there were fewer than two adult males available for a female to interact with.

Table A1
Summary of social groups, study subjects and observation periods

Group ID	Females[a]	Males[a]	Genetic ancestry[b]	Months in grooming data set[c]		Months in proximity data set[c]		Observation period[d]	Observation months[e]
				Per female	Per male	Per female	Per male		
1.1	33	48	0.20 ± 0.24 (0.03–0.87)	21.88 ± 13.60	28.02 ± 23.40	30.06 ± 18.76	28.04 ± 23.38	November 1999–September 2010	119
1.11	17	23	0.28 ± 0.26 (0.03–0.80)	14.53 ± 8.19	20.52 ± 18.07	21.25 ± 6.81	21.09 ± 18.54	May 2011–December 2015	56
1.12	5	9	0.16 ± 0.20 (0.03–0.72)	10.40 ± 1.67	9.22 ± 5.83	12.00 ± 2.00	9.22 ± 5.83	May 2011–November 2012	19
1.21	12	24	0.26 ± 0.29 (0.03–0.88)	17.78 ± 10.74	13.25 ± 13.60	19.27 ± 12.78	13.46 ± 14.04	November 1999–September 2008	72
1.211	8	13	0.32 ± 0.26 (0.04–0.89)	16.50 ± 7.07	19.31 ± 10.55	19.75 ± 7.59	19.38 ± 10.52	August 2012–December 2015	41
1.22	25	35	0.36 ± 0.28 (0.04–0.88)	31.84 ± 18.97	29.80 ± 26.77	38.08 ± 21.60	30.29 ± 27.19	November 1999–November 2012	145
1.221	8	9	0.38 ± 0.29 (0.04–0.90)	6.33 ± 2.34	9.56 ± 5.10	11.25 ± 1.83	11.56 ± 4.82	June 2014–December 2015	19
1.222	11	9	0.39 ± 0.30 (0.04–0.81)	7.27 ± 2.57	12.22 ± 7.03	8.91 ± 2.74	12.89 ± 7.37	June 2014–December 2015	19
2.1	20	44	0.26 ± 0.25 (0.03–0.82)	27.50 ± 20.01	24.23 ± 19.73	32.50 ± 24.96	24.68 ± 19.89	November 1999–March 2011	124
2.11	12	21	0.33 ± 0.27 (0.04–0.92)	15.80 ± 7.08	17.67 ± 13.44	20.17 ± 5.75	18.14 ± 13.64	June 2011–December 2015	55
2.12	8	10	0.32 ± 0.28 (0.03–0.82)	6.33 ± 1.97	9.40 ± 6.98	8.75 ± 3.01	9.90 ± 7.36	June 2011–November 2012	18
2.2	31	48	0.43 ± 0.30 (0.04–0.92)	25.42 ± 13.54	29.27 ± 26.48	31.19 ± 15.62	29.52 ± 26.66	November 1999–September 2011	121

[a] Number of unique individuals included in this data set, per unique social group. Individuals may be represented in more than one social group because of social group fissions and fusions and/or secondary dispersal by males.
[b] Mean ± SD (minimum–maximum).
[c] Mean ± SD. Due to our filtering criteria, individuals had to be in each data set for at least 8 months, but could be counted as members of different social groups across those months.
[d] The observation starting and ending month and year for each social group across both grooming and proximity data sets. Some observation periods span time periods in which behavioural monitoring was inconsistent or when social groups were too unstable (i.e. social groups were fissioning or fusing) to unambiguously determine an individual's group membership. For our analysis, we excluded these time periods as well as the 2009 hydrological year (1 November 2008–31 October 2009). We also excluded months when the number of adult males in the social group was less than two.
[e] The number of unique observation months for each social group included across the grooming and proximity data sets.

Table A2
Pearson's product-moment correlation (r) between predictor variables in the final grooming data set

	Genetic ancestry	Assortative genetic ancestry index	Heterozygosity		Genetic relatedness	Dominance rank		Female age	Adults in social group		Reproductive state	Pair co-residency	Observer effort
	Male		Female	Male		Female	Male		Female	Male			
Genetic ancestry													
Female	**0.098**	**−0.391**	**0.282**	**0.070**	**−0.086**	**0.027**	**0.028**	−0.009	**0.189**	**0.110**	**0.020**	**−0.053**	**−0.054**
Male		**−0.612**	**0.048**	**0.292**	**−0.158**	**0.047**	*−0.016*	**0.036**	**0.115**	**0.108**	−0.002	**0.042**	**−0.062**
Assortative genetic ancestry index			**−0.131**	**−0.159**	**0.244**	**−0.035**	**−0.069**	−0.001	**−0.090**	**−0.082**	0.001	**−0.044**	*0.017*
Heterozygosity													
Female				**0.044**	**−0.091**	**0.185**	**0.067**	*−0.015*	**0.205**	**0.151**	0.005	**−0.034**	**−0.152**
Male					**−0.086**	**0.020**	0.010	0.009	**0.056**	**0.077**	−0.013	0.000	**−0.042**
Genetic relatedness						0.011	**−0.045**	−0.005	**−0.030**	**−0.029**	−0.002	**0.033**	0.010
Dominance rank													
Female							**0.167**	−0.007	**0.396**	**0.335**	**0.026**	**0.039**	**−0.255**
Male								0.014	**0.399**	**0.505**	**−0.028**	**−0.033**	**−0.220**
Female age									**0.025**	**0.021**	**0.068**	**0.076**	**−0.064**
Adults in social group													
Female										**0.804**	*0.018*	**−0.029**	**−0.614**
Male											**−0.050**	**0.039**	**−0.436**
Reproductive state												**−0.027**	*0.017*
Pair co-residency													**0.026**

Predictor variables for which $P < 0.01$ are bolded and $0.01 < P < 0.05$ are italicized.

Table A3
Pearson's product-moment correlation (r) between predictor variables in the final proximity data set

	Genetic ancestry	Assortative genetic ancestry index	Heterozygosity		Genetic relatedness	Dominance rank		Female age	Adults in social group		Reproductive state	Pair co-residency	Observer effort
	Male		Female	Male		Female	Male		Female	Male			
Genetic ancestry													
Female	**0.095**	**−0.390**	**0.253**	**0.071**	**−0.086**	−0.008	**0.021**	0.001	**0.160**	**0.098**	0.011	**−0.032**	**−0.040**
Male		**−0.655**	**0.050**	**0.272**	**−0.164**	**0.032**	**−0.021**	**0.039**	**0.102**	**0.090**	−0.001	**0.053**	**−0.052**
Assortative genetic ancestry index			**−0.124**	**−0.163**	**0.237**	*−0.016*	**−0.056**	−0.008	**−0.068**	**−0.060**	0.001	**−0.056**	0.011
Heterozygosity													
Female				**0.045**	**−0.086**	**0.190**	**0.045**	**−0.027**	**0.189**	**0.116**	−0.004	**−0.028**	**−0.148**
Male					**−0.087**	*0.016*	0.000	*0.015*	**0.056**	**0.074**	−0.009	0.003	**−0.045**
Genetic relatedness						**0.020**	**−0.041**	0.002	*−0.017*	*−0.015*	0.002	**0.036**	0.001
Dominance rank													
Female							**0.150**	0.013	**0.378**	**0.304**	**0.066**	**0.029**	**−0.253**
Male								**0.050**	**0.375**	**0.491**	**−0.026**	**−0.037**	**−0.222**
Female age									**0.089**	**0.095**	**0.070**	**0.077**	**−0.101**
Adults in social group													
Female										**0.781**	*0.016*	**−0.028**	**−0.637**
Male											**−0.051**	**0.035**	**−0.451**
Reproductive state												*−0.016*	0.002
Pair co-residency													**0.022**

Predictor variables for which $P < 0.01$ are bolded and $0.01 < P < 0.05$ are italicized.

Encoding female reproductive state

In the main text, we report results for grooming and proximity behaviour from models where female reproductive state was coded as -1 for pregnancy and 1 for lactation. This deviates from the usual arbitrary coding of binary states as 0/1. We made this decision because we found that, with the 0/1 encoding, our beta and P value estimates for some model parameters depended on whether we assigned pregnancy to the 0 state versus lactation. Using the -1/1 alternative encoding eliminated this issue, produced consistent results across R packages ('glmmTMB' (version 1.0.0; Brooks et al., 2017) versus 'lme4' (version 1.1.23; Bates, Mächler, Bolker, & Walker, 2015)), and also qualitatively matched our estimates using a fixed effects-only model (using the function 'glm' from base R). Hence, we report the results using the -1/1 encoding in the main text.

Visualizing model effects

For a subset of figures, we plotted the probability of grooming and proximity behaviour as a function of a varying predictor of interest and model estimates assuming average values for all other covariates (Figs 1b, 1d, 2, 3, Appendix, Figs A2b, A2d, A3, A4). For example, to calculate the probability of grooming and proximity as a function of male dominance rank, we modelled an 'average' male (apart from his rank) interacting with an 'average' female in an 'average' demographic environment. We then estimated how variation in male rank is predicted to affect the probability of grooming or proximity using R's 'predict' function. For predictors that reflect the combined characteristics of the male–female pair, we used the same approach, but extended it to vary the characteristic of interest for both the male and the female, while holding the other predictor variables constant at their average value.

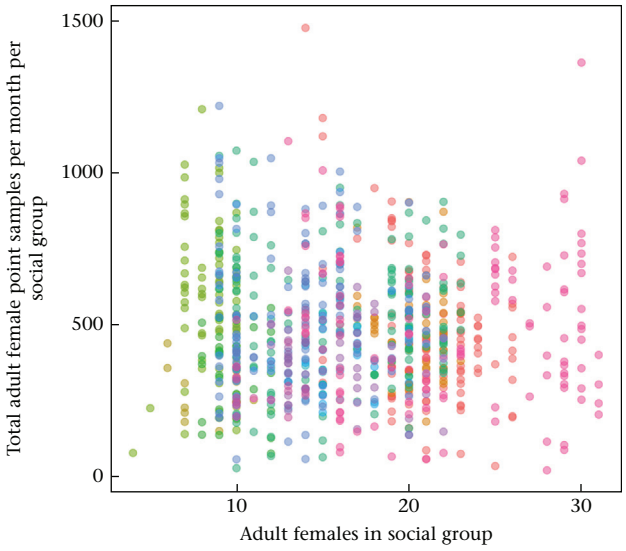

Figure A1. The total effort invested in behavioural observations across study groups of different sizes. Each dot represents a unique social group–month combination, coloured by social group ($N = 12$ social groups, $N = 812$ total group-months from the initial, monthly based data set). There is no relationship between the number of adult females present in a social group and the total number of point samples recorded for adult females per social group (10 point samples are collected per focal sample, if the sample is complete; linear model estimate for the effect of number of adult females on total number of point samples: $\beta = -1.615$, $P = 0.221$). The result is that observer effort per group does not vary by group size, but observer effort per individual baboon does. Hence, the probability of observing whether a given male–female dyad groomed or were in proximity at least once in a given time interval is smaller for large groups than for small groups. To address this problem, we included a measure of observer effort (total adult female point samples per social group/total adult females present in social group) in our models.

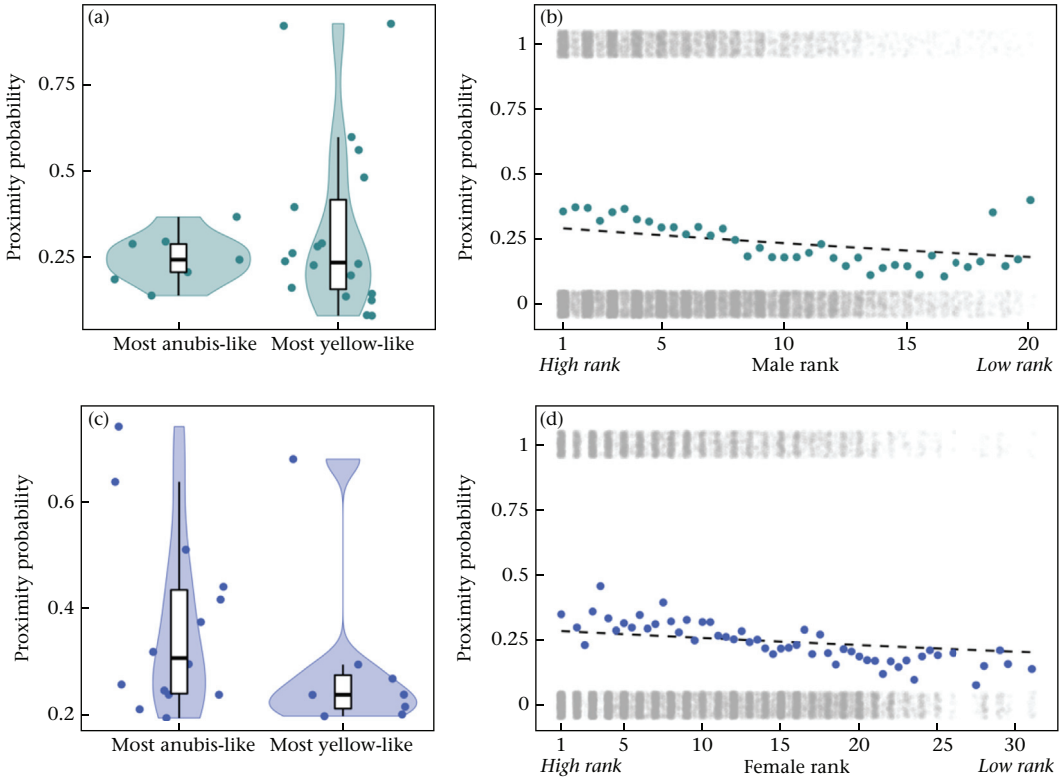

Figure A2. The influence of genetic ancestry and dominance rank on the tendency to be in proximity to an opposite-sex partner. (a) The probability of being in proximity among co-resident opposite-sex pairs, per 2-month interval, for the most anubis-like males (above the 90th percentile for male genetic ancestry in the data set, >81.5% anubis ancestry, $N = 9$ males) and the most yellow-like males (below the 10th percentile for male genetic ancestry in the data set, <4.8% anubis ancestry, $N = 20$ males). Probabilities are shown here based on the data without adjustment for other covariates (note that, although not visually apparent in the 1/0 proximity data as summarized here, more anubis-like males are more likely to be observed in proximity with female partners in the full model: $\beta = 0.270$, $P < 0.001$, Table 2). (b) The probability of being in proximity among co-resident opposite-sex pairs, per 2-month interval, as a function of male dominance rank. Coloured dots show probabilities based on counts of proximity occurrences, without adjustment for other covariates (as in (a)), and the dashed line shows the predicted relationship based on model estimates, assuming average values for all other covariates (see Appendix, Additional Methods). Grey dots show the presence ($y = 1$) or absence ($y = 0$) of proximity behaviour for all 21 130 female–male pair–interval combinations, as a function of male dominance rank (dots are jittered vertically for visibility). Noninteger values correspond to individuals that changed ranks during a 2-month interval in the data set. (c) As in (a), for the most anubis-like females (above the 90th percentile for female genetic ancestry in the data set, >74.1% anubis ancestry, $N = 14$ females) and the most yellow-like females (below the 10th percentile for female genetic ancestry in the data set, <3.2% anubis ancestry, $N = 8$ females). (d) As in (b), with the probability of being in proximity shown as a function of female dominance rank.

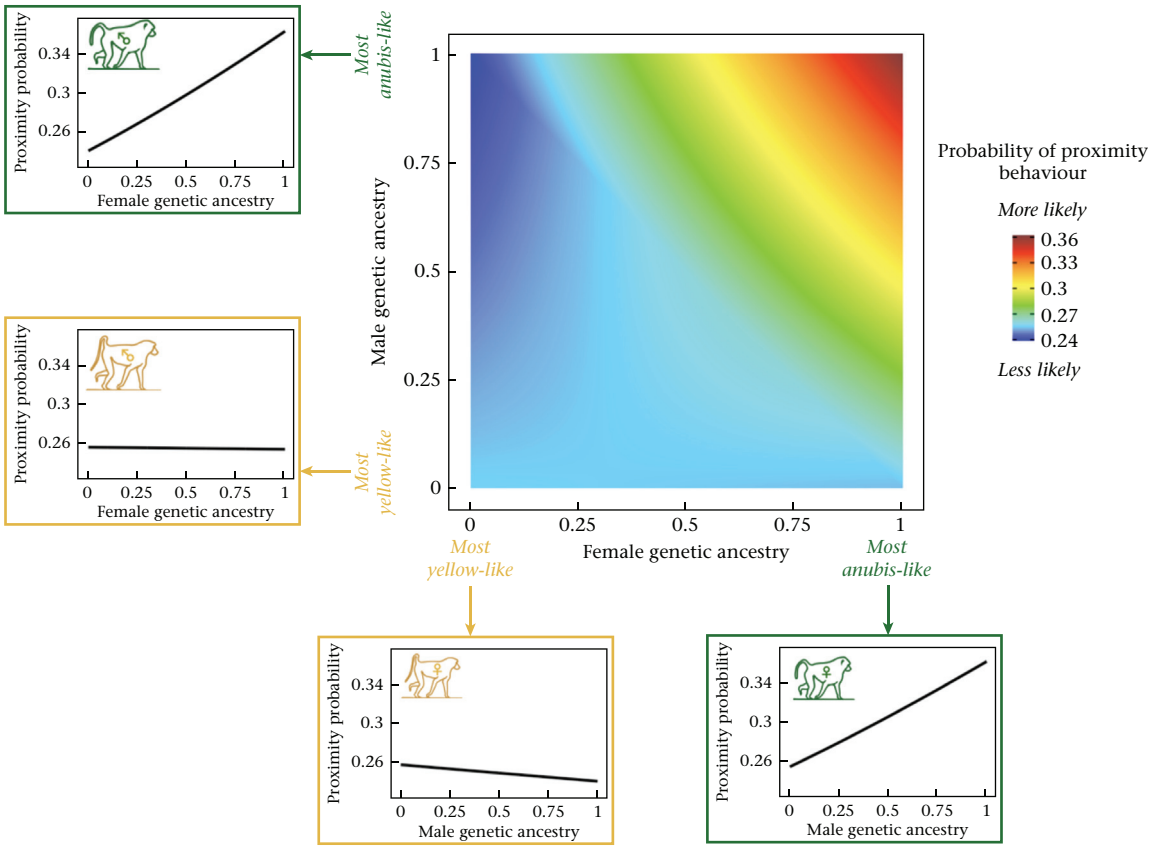

Figure A3. The combined effect of genetic ancestry characteristics of females and males on the probability of being in proximity. The central heatmap shows the probability of proximity behaviour as a function of female genetic ancestry (*X* axis) and male genetic ancestry (*Y* axis), based on model estimates assuming average values for all other covariates (see Appendix, Additional Methods). Assortative affiliative behaviour is reflected by the increased probability of yellow-like females being in proximity with yellow-like males, relative to anubis-like males, and anubis-like females being in proximity with anubis-like males, relative to yellow-like males. The probability of being in proximity is highest for pairs where both partners are anubis-like. Line graphs surrounding the heatmap show model predictions for the probability of proximity behaviour for males (left) and females (bottom) at the two extremes of genetic ancestry, as a function of the genetic ancestry of potential opposite-sex social partners.

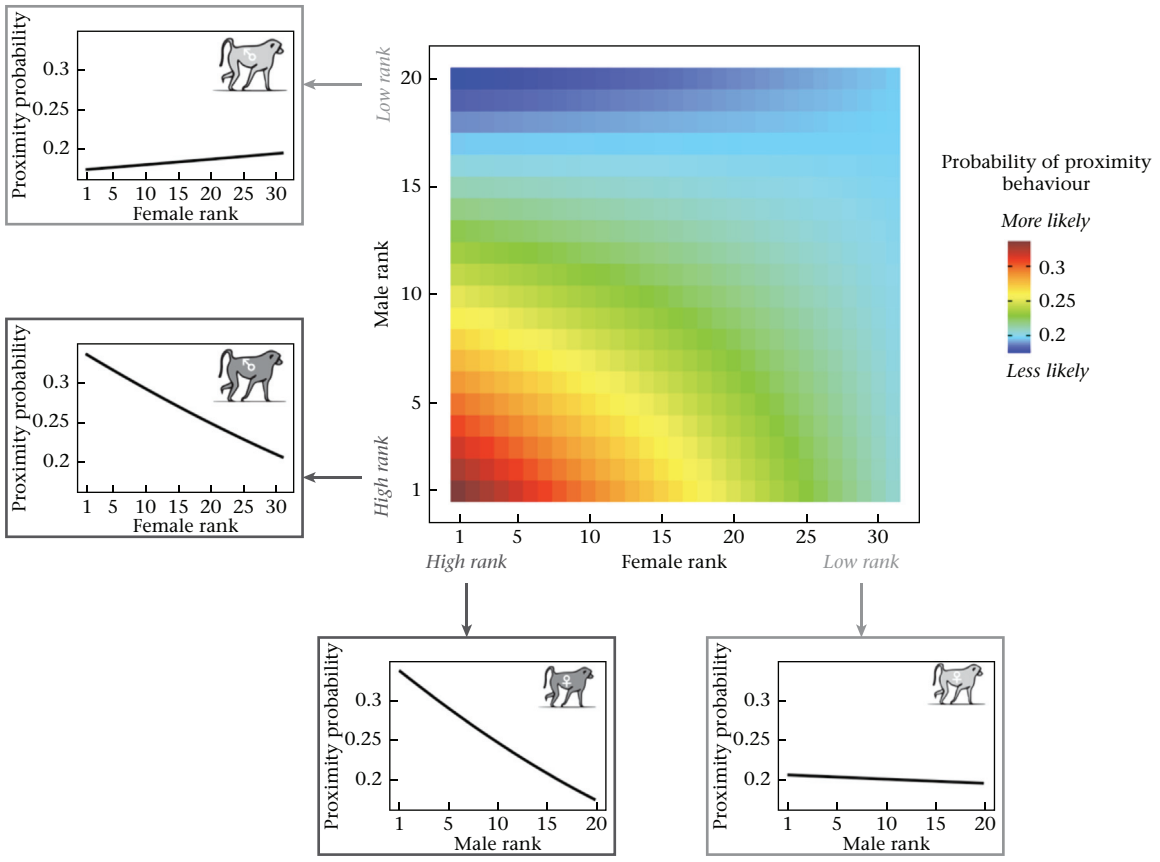

Figure A4. The combined effect of rank characteristics of females and males on the probability of being in proximity. The central heatmap shows the probability of proximity behaviour as a function of female dominance rank (*X* axis) and male dominance rank (*Y* axis), based on model estimates assuming average values for all other covariates (see Appendix, Additional Methods). The probability of being in proximity is highest for pairs where both partners are high ranking. Line graphs surrounding the heatmap show model predictions for the probability of proximity behaviour for males (left) and females (bottom) at the extremes of the rank distribution, as a function of the dominance rank of potential opposite-sex social partners.

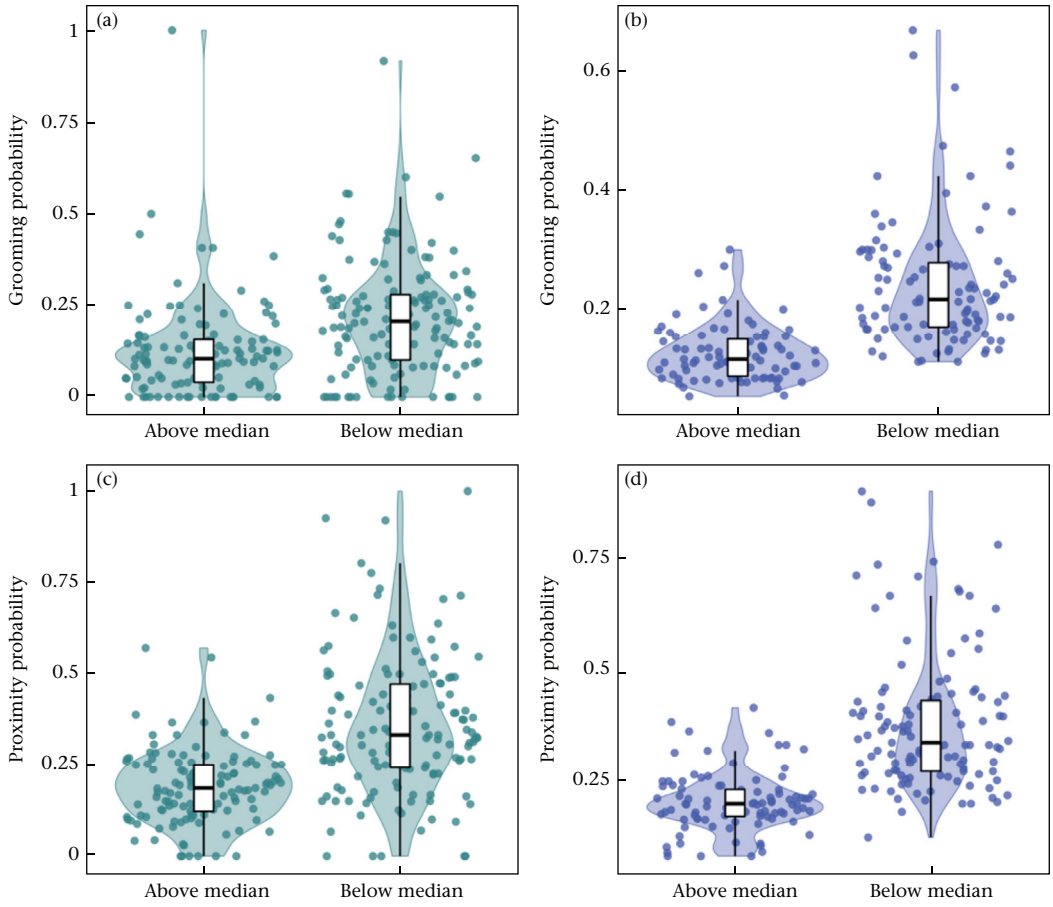

Figure A5. The influence of the number of adult males present in a social group on grooming and proximity behaviour. (a, b) The probability of grooming among co-resident opposite-sex pairs, per 2-month interval, for each male (a) and female (b) in social groups with greater or less than the median number of co-resident males in the sample ($N = 12$ males). Probabilities are shown here based on the data without adjustment for other covariates. (c, d) As in (a, b), for proximity behaviour (median = 11.5 males).

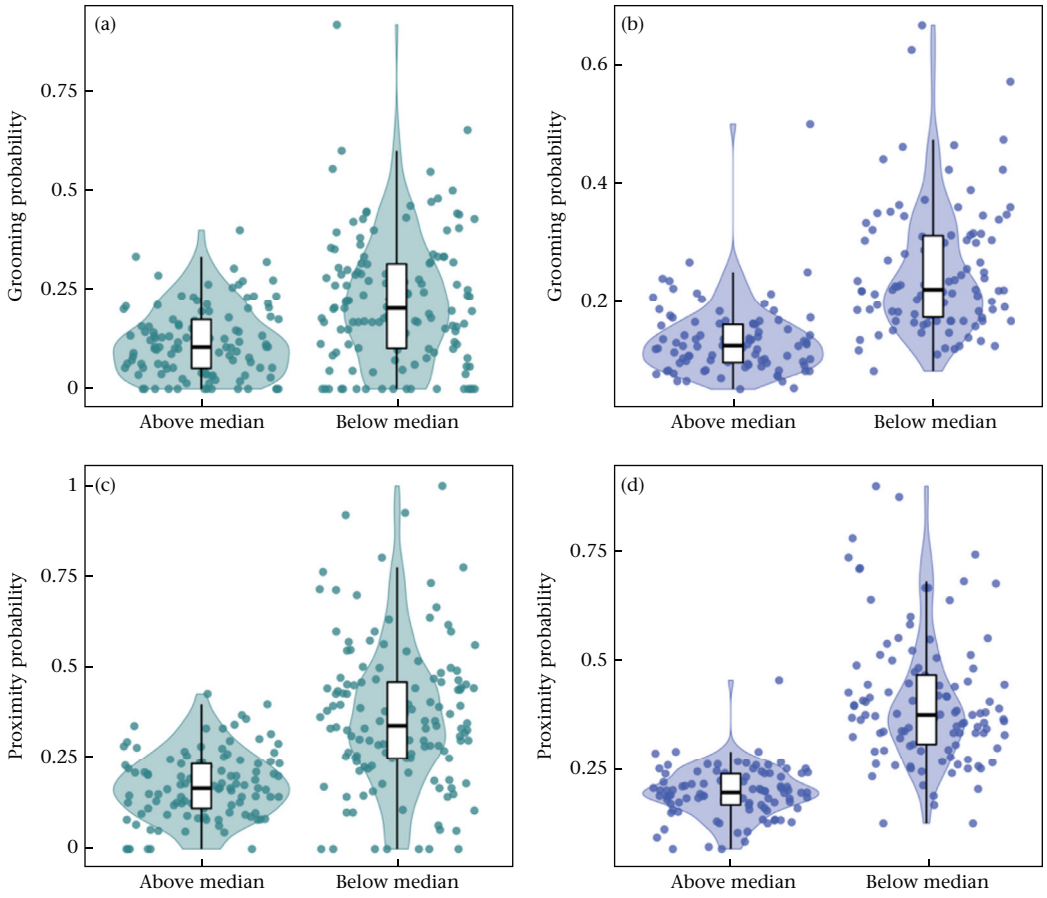

Figure A6. The influence of the number of adult females present in a social group on grooming and proximity behaviour. (a, b) The probability of grooming among co-resident opposite-sex pairs, per 2-month interval, for each male (a) and female (b) in social groups with greater or less than the median number of co-resident females in the sample ($N = 20$ females). Probabilities are shown here based on the data without adjustment for other covariates. (c, d) As in (a, b), for proximity behaviour (median = 20 females). Note that in the full model, the apparent difference observable for proximity was not significant after taking into account other model covariates and random effects ($\beta = -0.018$, $P = 0.073$; Table 2).