

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

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1 **ABSTRACT**

2       Opposite-sex social relationships are important predictors of fitness in many animals,  
3 including several group-living mammals. Consequently, understanding sources of variance in the  
4 tendency to form opposite-sex relationships is important for understanding social evolution.  
5 Genetic contributions are of particular interest due to their importance in long-term evolutionary  
6 change, but little is known about genetic effects on male-female relationships in social mammals,  
7 especially outside of the mating context. Here, we investigate the effects of genetic ancestry on  
8 male-female affiliative behavior in a hybrid zone between the yellow baboon (*Papio*  
9 *cynocephalus*) and the anubis baboon (*P. anubis*), in a population in which male-female social  
10 bonds are known predictors of lifespan. We place our analysis within the context of other social  
11 and demographic predictors of affiliative behavior in baboons. Genetic ancestry was the most  
12 consistent predictor of opposite-sex affiliative behavior we observed, with the exception of  
13 strong effects of dominance rank. Our results show that increased anubis genetic ancestry is  
14 associated with subtly, but significantly higher rates of opposite-sex affiliative behavior, in both  
15 males and females. Additionally, pairs of anubis-like males and anubis-like females were the  
16 most likely to socially affiliate, resulting in moderate assortativity in grooming and proximity  
17 behavior as a function of genetic ancestry. Our findings indicate that opposite-sex affiliative  
18 behavior partially diverged during baboon evolution to differentiate yellow and anubis baboons,  
19 despite overall similarities in their social structures and mating systems. Further, they suggest  
20 that affiliative behavior may simultaneously promote and constrain baboon admixture, through  
21 additive and assortative effects of ancestry, respectively.

22 **KEYWORDS**

23 baboon; genetic ancestry; grooming; hybrid zone; opposite-sex social bonds; *Papio anubis*;  
24 *Papio cynocephalus*

25 **HIGHLIGHTS**

- 26 • Opposite-sex social relationships can have important fitness consequences.  
27 • In hybrid baboons, genetic ancestry predicted male-female affiliative behavior.  
28 • Both an individual's genetic ancestry and that of its social partner mattered.  
29 • Male-female affiliation was assortative with respect to genetic ancestry.  
30 • Dominance rank and group demography also influenced male-female social affiliation.

31 Social relationships, both within and between sexes, are ubiquitous features in the lives of  
32 social mammals. Affiliative interactions among members of the same sex are positively  
33 associated with fertility or survival in a number of social mammal species, including group-  
34 living primates, equids, cetaceans, and rodents (e.g., Cameron et al., 2009; Ellis et al., 2019;  
35 Frère et al., 2010a; Schülke et al., 2010; Silk et al., 2009, 2010; Weidt et al., 2008). Opposite-sex  
36 affiliative bonds can also have important consequences. In monogamous species, strong social  
37 bonds between sexual partners predict shorter interbirth intervals, increased offspring number,  
38 and improved offspring survival, potentially due to improved coordination between partners in  
39 caring for young, obtaining resources, or defense against predators (e.g., Black, 2001; Griggio &  
40 Hoi, 2011; Ribble, 1992; Sánchez-Macouzet et al., 2014). Further, in some group-living  
41 primates, females compete for access to males outside of mating contexts, suggesting that social  
42 bonds with males are themselves an important resource (Archie et al., 2014; Baniel et al., 2016,  
43 2018; Cheney et al., 2012; Haunhorst et al., 2019; Lemasson et al., 2008; Palombit et al., 2001;  
44 Seyfarth, 1978). In support of this idea, females in several cercopithecine monkey species benefit  
45 from opposite-sex social bonds via enhanced survival, care for their offspring, and protection  
46 from harassment (Archie et al., 2014; Baniel et al., 2016; Haunhorst et al., 2017; Kulik et al.,  
47 2012; Lemasson et al., 2008; Moscovice et al., 2009; Nguyen et al., 2009; Palombit et al., 1997;  
48 Seyfarth, 1978; Silk et al., 2020; Weingrill, 2000). Males of these species may also benefit from  
49 social bonds with females. For example, baboon males who form strong social bonds with  
50 females tend to live longer than those who do not (Campos et al., 2020). Males may also benefit  
51 by gaining mating opportunities (although the evidence for this benefit is mixed), opportunities  
52 to care for their offspring, or access to infants that can be exploited for social gain (Ménard et al.,  
53 2001; Packer, 1979b; Smuts, 1985; van Schaik & Paul, 1996; Whitten, 1987).

54 While a number of studies have investigated the sources of variance in same-sex  
55 affiliative relationships in group-living mammals (Best et al., 2014; Frère et al., 2010b;  
56 Langergraber et al., 2009; Mitani, 2009; Möller et al., 2001; Seyfarth, 1976; Seyfarth et al.,  
57 2014; Silk et al., 2006a; Silk et al., 2006b; Smith et al., 2006; Widdig et al., 2001), we know  
58 comparably less about the sources of variance in opposite-sex relationships, especially outside  
59 the mating context. Addressing this gap is important for understanding the evolution of  
60 heterosexual bonds. In particular, if the tendency to form opposite-sex social bonds is affected by  
61 genotype, it has the potential to evolve in response to natural selection. Strong evidence for  
62 genetic effects comes from interspecific comparisons between pair-bonded and multiply mating  
63 species. For example, comparisons between the monogamous prairie vole and other, closely  
64 related promiscuous voles have identified genetic divergence in the pathways that regulate  
65 arginine vasopressin, oxytocin, and dopamine signaling, which in turn influences pair-bonding  
66 behavior (Young et al., 1996; Young et al., 1999; Young et al., 1997a; Young et al., 1997b;  
67 reviewed in Carter & Perkeybile, 2018; Johnson & Young, 2015; Sadino & Donaldson, 2018;  
68 Young et al., 2011). These pathway differences may in part be due to differences in the  
69 distribution and densities of hormone receptors in the brain, suggesting one important  
70 mechanism through which variation in opposite-sex social relationships evolves (Insel &  
71 Shapiro, 1992; Insel et al., 1994; Smeltzer et al., 2006). Research in other pair-bonded rodents,  
72 primates, fish, frogs, and birds has placed these findings in a broader context, indicating that  
73 these and other pathways (e.g., Young et al., 2019) consistently influence pair-bonding across  
74 divergent species, although they may do so in a species-specific manner (reviewed in Carter &  
75 Perkeybile, 2018; Fischer et al., 2019a; Johnson & Young, 2015).

76 Despite these important discoveries in pair-bonded species, little is known about genetic  
77 influences on opposite-sex social bonding in group-living animals, including the degree to which  
78 genotype contributes to differences between species with similar social and mating systems.  
79 Here, we investigate the association between genetic ancestry and male-female affiliative  
80 behavior in a well-studied natural primate population, the baboons of Kenya’s Amboseli basin  
81 (Alberts, 2018; Alberts & Altmann, 2012). Baboons (genus *Papio*) began speciating ~1.4 million  
82 years ago, and today, the six extant species occupy distinct geographic ranges across Africa  
83 (Rogers et al., 2019). Most species of baboons, including those in Amboseli, live in multi-male,  
84 multi-female social groups in which multiple individuals of both sexes mate and form social  
85 bonds (Fischer et al., 2019b). Amboseli lies in a hybrid zone between two such species, the  
86 yellow baboon (*Papio cynocephalus*) and the anubis baboon (*P. anubis*, also known as the olive  
87 baboon) (Alberts & Altmann, 2001; Samuels & Altmann, 1986; Tung et al., 2008; Wall et al.,  
88 2016). While yellow baboons contribute the majority of genetic ancestry in this population, the  
89 range of admixture we observe—from animals that are almost entirely yellow to those that are  
90 almost entirely anubis—gives us the opportunity to examine potential genetic ancestry effects on  
91 opposite-sex affiliative relationships. Complementary data on social and demographic variables  
92 for the same individuals allow us to place these effects in the context of other, environmental  
93 sources of variance.

#### 94 *Genetic ancestry effects on male-female interactions in hybrid zones*

95 The Amboseli baboon hybrid zone provides a “natural laboratory” for understanding the  
96 relationship between genetic ancestry and affiliative behavior because it allows individuals with  
97 varying admixed genomes to be observed in a shared environment (Hewitt, 1988). In turn,  
98 studying social behavior in hybrid zones can shed light onto hybrid zone dynamics, as most  
99 clearly illustrated in cases where ancestry influences mating behavior. In such cases, assortative  
100 mating by ancestry limits gene flow and can reinforce species boundaries, whereas ancestry-  
101 related mating advantages can lead to asymmetric gene flow and range expansion (e.g.,  
102 Baldassarre & Webster, 2013; Baldassarre et al., 2014; Kronforst et al., 2006; Mavárez et al.,  
103 2006).

104 Ancestry effects on mating behavior have also been detected in both the yellow baboon-  
105 anubis baboon hybrid zone in Amboseli and in an anubis baboon-hamadryas baboon hybrid zone  
106 in Ethiopia. In Amboseli, anubis-like males are more likely to obtain consortships (extended  
107 mate-guarding associations between an adult male and an adult female in estrus, during which  
108 most conceptions occur), and male-female pairs with similar genetic ancestry are more likely to  
109 consort than pairs with different ancestry (Tung et al., 2012). In the Ethiopian hybrid zone,  
110 ancestry affects both male mating strategy and how females respond to males (Bergman &  
111 Beehner, 2003). However, we do not yet understand whether genetic ancestry effects extend to  
112 other aspects of male-female interactions, such as affiliation between male-female pairs outside  
113 of the mating context (but see Bergman et al., 2008 for an analysis of male interest in non-estrus  
114 females). If so, genetic ancestry effects on male-female social relationships may be more  
115 important than indicated by analyses of mating behavior alone. Specifically, because opposite-  
116 sex social affiliation also predicts lifespan in the Amboseli population (Archie et al., 2014;  
117 Campos et al., 2020), ancestry effects on this trait may secondarily affect how long individuals  
118 live and who they co-reside with, thus influencing the genetic composition of subsequent  
119 generations.

120 *Goals of this study*

121 Here, we evaluated the extent to which genetic ancestry predicts the formation of male-  
122 female social relationships in baboons. We focused specifically on male-female affiliative  
123 behavior in non-mating contexts (i.e., periods when females were pregnant or lactating, and not  
124 sexually cycling) because social relationships in these contexts are not driven by immediate  
125 sexual interactions. Using two multivariate models (one for grooming behavior and one for  
126 proximity behavior), we simultaneously tested for (i) the additive effects of male and female  
127 individual characteristics, including genetic ancestry, on the probability of affiliative social  
128 behavior between males and females, and (ii) characteristics defined by the pair, including  
129 ancestry-related assortativity. In the same model, we also tested two additional hypotheses: (iii)  
130 that opposite-sex affiliation depends on female reproductive state (i.e., pregnancy or lactation),  
131 based on evidence that the stability of male-female relationships varies across baboon species as  
132 a function of female reproductive state (Baniel et al., 2016; Fischer et al., 2017; Goffe et al.,  
133 2016; Nguyen et al., 2009; Städele et al., 2019; Weingrill, 2000); and (iv) that opposite-sex  
134 affiliation depends on group demography, based on findings that male-female interactions in  
135 baboons and other primates also depend on group composition (Archie et al., 2014; Bergman &  
136 Beehner, 2003; Rosenbaum et al., 2016; Tung et al., 2012).

137 **METHODS**

138 *Study subjects*

139 Study subjects were adult baboons from an intensively studied wild population inhabiting  
140 the Amboseli ecosystem of southern Kenya (Alberts, 2018; Alberts & Altmann, 2012). This  
141 population consists of multigeneration hybrids, most of which have predominantly yellow  
142 baboon ancestry, but some of which are recent hybrid descendants of anubis or anubis-like  
143 immigrants that have arrived in Amboseli since the early 1980's (approximately a decade after  
144 long-term observations began) (Alberts & Altmann, 2001; Charpentier et al., 2008; Samuels &  
145 Altmann, 1986; Tung et al., 2008; Wall et al., 2016). This natural hybrid population is situated  
146 within a narrow hybrid zone that likely extends along the geographic boundary between yellow  
147 baboon and anubis baboon distributions in East Africa (Charpentier et al., 2012).

148 Members of the Amboseli baboon study population are individually recognized based on  
149 physical appearance and are monitored on a near-daily basis by trained observers who record  
150 demographic data (e.g., group membership, births, deaths, immigration, emigration) and  
151 behavioral data (e.g., social interactions, mating, traveling, resting, feeding). Study subjects were  
152 parous adult females (because parous females are strongly preferred over nulliparous females as  
153 mates by adult males of most primate species: Anderson, 1986; Gesquiere et al., 2007) and adult  
154 males that had achieved a social dominance rank among other adult males in their group (Table  
155 S1). Overall, we considered members of twelve social groups that were studied between  
156 November 1999 and December 2015. We restricted the data set to include only males and  
157 females for whom estimates of genetic ancestry, genetic diversity, and genetic relatedness  
158 between individuals in male-female pairs could be calculated from previously generated  
159 microsatellite data (Buchan et al., 2003; Tung et al., 2008; Tung et al., 2012). The resulting  
160 sample contained 136 females and 160 males, who together formed 3,468 unique male-female  
161 dyads across the grooming and proximity data sets.

162 *Affiliative social behavior*

163 Grooming and maintenance of close spatial proximity (hereafter, proximity) are  
164 affiliative behaviors important to establishing, maintaining, and strengthening social bonds in  
165 non-human primates (Cords, 1997; Cords, 2012; Palombit et al., 1997; Silk et al., 2013).  
166 Although male-female grooming and proximity events were moderately correlated in our data set  
167 (Pearson's product-moment correlation:  $r = 0.222$ ,  $P < 10^{-15}$ ), we analyzed grooming and  
168 proximity separately because grooming measures only explained 4.9% of the variance in the  
169 proximity data. Grooming data were collected during systematic monitoring of the population,  
170 following a sampling protocol in which observers move in a predetermined random order  
171 throughout the group. This approach avoids biases due to uneven sampling of subjects (Alberts  
172 et al., 2020; Archie et al., 2014). Proximity data were collected during random-order focal  
173 animal sampling on adult females, during which the identity of the nearest adult male within 5  
174 meters, if any, was recorded once per minute for the duration of each 10 minute sample (Alberts  
175 et al., 2020). We excluded data from time periods in which behavioral monitoring was  
176 inconsistent or when social groups were too unstable (i.e., social groups were fissioning or  
177 fusing) to unambiguously determine an individual's group membership. We also excluded all  
178 data from the 2009 hydrological year (November 1<sup>st</sup>, 2008-October 31<sup>st</sup>, 2009) which included  
179 the most severe drought documented in the Amboseli basin in more than 40 years (Okello et al.,  
180 2016; Tuqa et al., 2014). Omitting data from 2009 ensured that effects from this rare and extreme  
181 event, which altered patterns of female fertility and reproductive states, did not influence our  
182 results (Fitzpatrick et al., 2014; Lea et al., 2015).

183 *Predictor variables*

184 We investigated the relationship between genetic ancestry and opposite-sex affiliative  
185 social behavior using the following predictors, motivated in part by known predictors of mating  
186 behavior in this population (Tung et al., 2012) (see Tables S2-S3 for correlations among all  
187 predictor variables).

188 *Genetic ancestry.* Genetic estimates of hybridity (i.e., the proportion of each individual's  
189 genome estimated to be from anubis ancestry) were included for females ( $h_f$ ) and males ( $h_m$ ).  
190 These estimates were based on genotypes at up to 13 highly polymorphic microsatellite markers  
191 and average ancestry assignments produced using the Bayesian clustering algorithm  
192 STRUCTURE 2.3.4 (Falush et al., 2003; Pritchard et al., 2000; see Tung et al., 2008; mean typed  
193 loci per individual =  $12.40 \pm 1.10$  s.d.). These assignments range continuously from 0 to 1, where  
194 0 corresponds to unadmixed yellow baboon ancestry and 1 corresponds to unadmixed anubis  
195 baboon ancestry. These estimates are strongly correlated with recent genome-wide ancestry  
196 estimates (Pearson's product-moment correlation:  $r = 0.717$ ,  $P = 1.17 \times 10^{-4}$ ,  $n=23$  individuals  
197 that overlapped between data sets) (Wall et al., 2016); however, because genome-wide estimates  
198 are available for only a subset of the population, we used the microsatellite-based estimates here.

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

204 
$$b = \max(h_m \times h_f, (1 - h_m) \times (1 - h_f))$$

205  
206 This index ranges from 0 to 1: high values indicate highly assortative male-female pairs (i.e.,  
207 individuals in the pair both have low or high genetic ancestry estimates) and low values indicate  
208 highly disassortative male-female pairs (i.e., individuals in the pair have different genetic  
209 ancestry estimates). Intermediate values indicate male-female pairs where both individuals are of  
210 intermediate ancestry.

211 *Heterozygosity.* High genetic diversity is sometimes thought to be a measure of genetic  
212 quality (Kempnaers, 2007). Because it is relevant to mate choice (Kempnaers, 2007) and  
213 potentially social partner choice, we therefore included a measure of genetic diversity for both  
214 males and females using up to 14 highly polymorphic microsatellite markers (mean typed loci  
215 per individual =  $13.13 \pm 1.22$  s.d.; 13 of these markers were also used to assign genetic ancestry  
216 scores). We estimated individual genetic diversity by dividing the number of heterozygous loci  
217 by the number of genotyped loci for each individual (following Charpentier et al., 2008).  
218 Importantly, there is no overall effect of species identity (i.e., yellow or anubis) on genetic  
219 diversity using these markers (Charpentier et al., 2012).

220 *Relatedness.* Because the formation of social bonds may be affected by kinship, we  
221 included an estimate of genetic relatedness for each male-female dyad using the method of  
222 Queller and Goodnight (1989). These estimates, based on the same genotype data used to  
223 estimate heterozygosity, were calculated using the function *coancestry* in the R package *related*  
224 (version 1.0; Pew et al., 2015; Wang, 2011).

225 *Social dominance rank.* Social dominance rank can enhance access to valuable resources,  
226 including desirable social partners (e.g., Archie et al., 2014; Baniel et al., 2016; Haunhorst et al.,  
227 2019; Lemasson et al., 2008; Palombit et al., 2001). We therefore modeled female rank, male  
228 rank, and the interaction between female and male ranks as additional fixed effects in the  
229 models. Female and male ranks were assigned separately for each sex, on a monthly basis, based  
230 on the outcomes of dyadic agonisms between all pairs of individuals in the same group (Alberts  
231 et al., 2020). We represented rank using an ordinal approach, where the highest-ranking  
232 individual holds rank 1 and lower-ranking individuals occupy ranks of successively higher  
233 numbers. Since female and male ranks were assigned on a monthly basis and our time window  
234 for analyses of grooming and proximity interactions spanned a two-month period, we used the  
235 average of each individual's rank across both months for each two-month interval.

236 *Age.* Female age may also affect a female's social interactions. To account for possible  
237 age-related effects, we modeled a linear effect of female age, averaged across each two-month  
238 analysis window (i.e., her age at the start of the second month), as a continuous predictor  
239 variable in our models. We also included a transformed measure of female age that reflects the  
240 relationship between female age and conception probability in this population, where the highest  
241 conception probability occurs at ~14 years of age (Beehner et al., 2006). Following Tung et al.  
242 (2012), we calculated female transformed age,  $a_t$ , as a function of  $a_u$ , the untransformed female  
243 age:

244

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

245

246 This transformation assigns 0 for the value of  $a_t$  at 14, the age at which conception probabilities  
247 are highest; values of  $a_t$  become increasingly negative with distance from age 14. For 90.4%  
248 (123 out of 136) of the females in the data set, birthdates were known to within a few days. For  
249 the other females in the data set, birthdates were estimated to within 6 months (i.e.,  $\pm 3$  months'  
250 error). Male age was not included in any models since it is tightly correlated with rank in male  
251 baboons (Alberts et al., 2003) and its effect on mating and social behavior is likely to be linked  
252 to rank (Silk et al., 2020; Tung et al., 2012).

253

254 *Group composition.* To incorporate group-level demographic effects on social behavior,  
255 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 two-month analysis period).

256

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

267

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

271

272 *Observer effort.* The number of field observers and the amount of time spent conducting  
273 behavioral observations for each study group was consistent across all study groups regardless of  
274 their size (Fig. S1). Consequently, the probability of observing grooming or proximity events  
275 could vary as a function of social group size, because an observer watching a small group is  
276 likely to capture a larger fraction of interactions in a given time period than that same observer  
277 watching a much larger group. Thus, we calculated observer effort and included it as a covariate  
278 in both models. Observer effort was estimated as the average number of minutes of focal sample  
279 data collected per adult female per social group in a given two-month interval (see  
Supplementary Methods).

280

281 *Statistical analyses*  
282 Grooming and proximity behavior were modeled as binary events and analyzed  
283 separately using binomial mixed effects models. Each row of data corresponded to a unique, co-  
resident female-male dyad in a given two-month interval, and was assigned a value of “1” if the



284 dyad was observed grooming or in proximity at least once during the two-month interval and a  
285 “0” if they were not. We used two months as our time interval because our resolution for  
286 grooming and proximity behavior is relatively coarse on a month-to-month basis, even after  
287 excluding months in which observer effort was low (see Supplementary Methods).

288 We retained all two-month intervals in which focal females groomed or were in  
289 proximity with any candidate male social partner at least once, except for: (i) two-month  
290 intervals in which females transitioned between reproductive states; and (ii) two-month intervals  
291 in which the average number of adult males in the social group was less than two. We also  
292 excluded any male in a female’s two-month interval if he was only present for one of the two  
293 months and excluded all data for females and males who were observed for less than 8 months  
294 because sparse data makes it difficult to estimate individual-level random effects. The final  
295 grooming data set included 127 unique females and 160 unique males across 1,866 female two-  
296 month intervals (17,356 female-male pair-interval combinations), and the final proximity data set  
297 included 131 unique females and 160 unique males across 2,338 female two-month intervals  
298 (21,130 total female-male pair-interval combinations).

299 We ran binomial mixed effects models using the function *glmmTMB* (family =  
300 “binomial”) in the R package *glmmTMB* (version 1.0.1; Brooks et al., 2017), using a logit link:

$$301 \quad y_{ij} \sim \text{Bin}(1, p_{ij})$$
$$302 \quad p_{ij} = \text{logit}(\beta_0 + \mathbf{X}_{ij}\boldsymbol{\beta} + m_i + f_i + \varepsilon_{ij})$$

303 where  $y_{ij}$  is a 0/1 value indicating whether male-female dyad  $i$  was observed grooming or in  
304 proximity during a two-month interval  $j$ .  $y_{ij}$  is drawn from a binomial distribution, where the  
305 probability of grooming or proximity ( $p_{ij}$ ) is modeled as the function of the logit-transformed  
306 sum of (i) the intercept,  $\beta_0$ ; (ii) the fixed effects ( $\mathbf{X}_{ij}\boldsymbol{\beta}$ ) of male genetic ancestry, female genetic  
307 ancestry, the assortative genetic ancestry index for that pair, male heterozygosity, female  
308 heterozygosity, genetic relatedness between individuals in that pair, male dominance rank,  
309 female dominance rank, female age, transformed female age, the number of adult females in the  
310 social group, the number of adult males in the social group, female reproductive state (pregnant  
311 or lactating), the interaction between female reproductive state and female genetic ancestry, the  
312 interaction between female reproductive state and male genetic ancestry, the interaction between  
313 male and female dominance ranks, pair co-residency, and observer effort ( $\mathbf{X}_{ij}$  represents all of  
314 these data using standard matrix notation and  $\boldsymbol{\beta}$  refers to the vector of all fixed effect estimates);  
315 and (iii) the random effects of male identity,  $m_i$ , and female identity,  $f_i$ .  $\varepsilon_{ij}$  represents model  
316 error.

317 To assess statistical significance, we used permutation tests to account for unequal  
318 representation of individuals in the data set and predictors that did not follow standard parametric  
319 distributions. We followed the procedure of Tung et al. (2012), who conducted a similar analysis  
320 on mating behavior. Specifically, we first computed, for each female-interval combination, the  
321 proportion of dyads where an event (grooming or proximity) occurred. These values are  
322 estimates of the probability of grooming or proximity with any male, per female-interval  
323 combination. These probabilities were then permuted across all female two-month intervals, and  
324 randomized response variables (0/1) were generated by drawing from a binomial distribution  
325 with  $p_{ij}$  equal to the permuted grooming or proximity probability for each female-interval. This  
326 approach preserves the structure of the predictor variables (including correlations between

327 predictors), the number of times each individual is represented in the data set, and the  
328 distribution of grooming or proximity events for each female-interval. We then fit the model  
329 used to analyze the real data to the permuted data set and calculated a p-value for each predictor  
330 variable based on the number of times that the absolute value of the effect size estimated from  
331 the permuted data sets was greater than the absolute value of the effect size estimated from the  
332 observed data set, across 1,000 permutations. All analyses were run in R (version 3.6.1; R Core  
333 Team, 2019).

#### 334 *Ethical note*

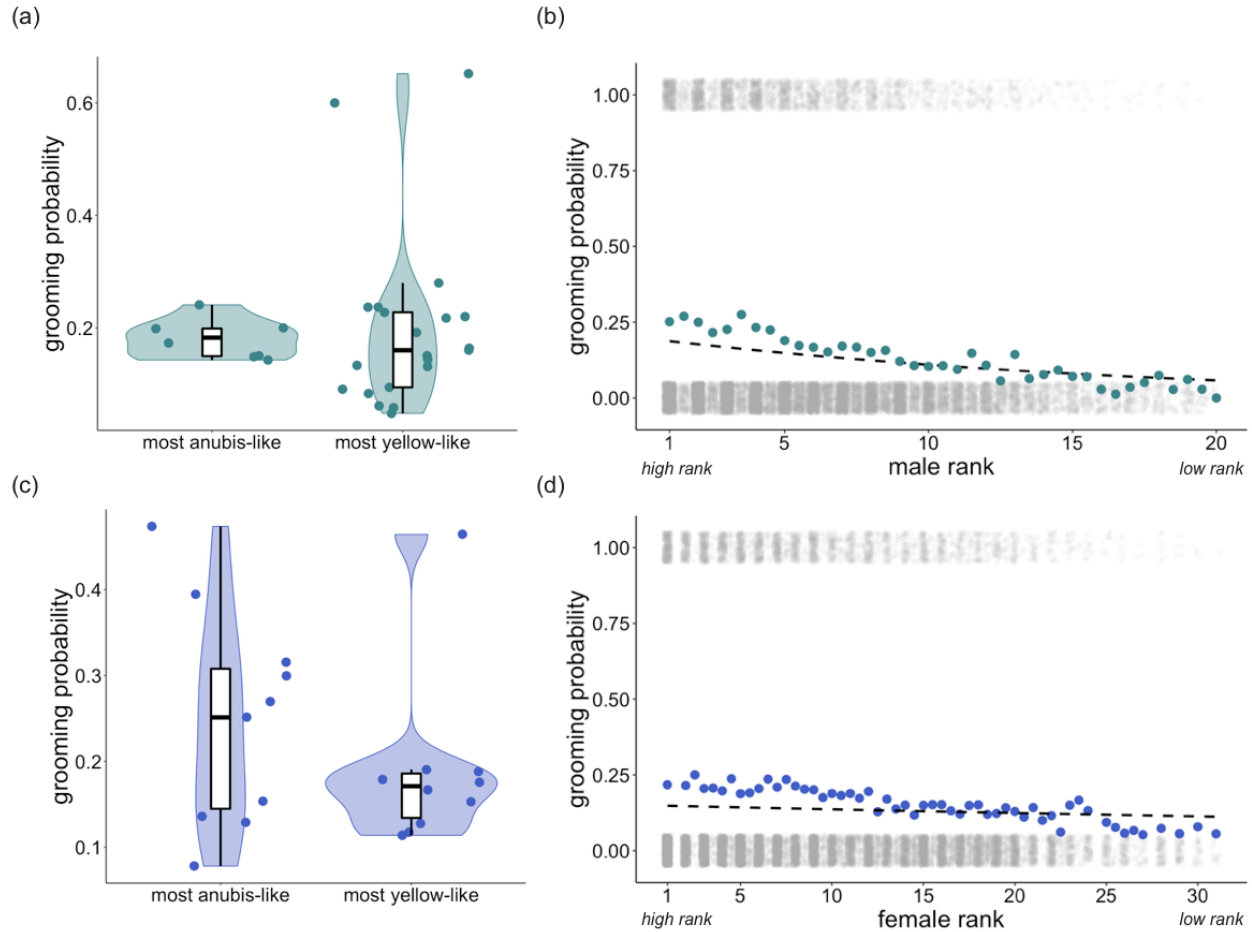
335 The research in this study was approved by the Institutional Animal Care and Use  
336 Committees (IACUC) at Duke University (#A273-17-12), and adhered to the laws and  
337 guidelines of the Kenyan government.

## 338 **RESULTS**

### 339 *Individual characteristics: genetic ancestry and dominance rank predict opposite-sex affiliative* 340 *social behavior in males and females*

341 Our models identified two male characteristics that consistently predicted opposite-sex  
342 grooming and proximity behavior (Tables 1-2). Specifically, grooming and proximity were more  
343 likely to occur if the male in the dyad had more anubis ancestry (grooming:  $\beta = 0.429$ ,  $p < 0.001$ ,  
344 Table 1, Fig. 1a; proximity:  $\beta = 0.270$ ,  $p < 0.001$ , Table 2, Fig. S2a) and was higher ranking  
345 (grooming:  $\beta = -0.096$ ,  $p < 0.001$ , Table 1, Fig. 1b; proximity:  $\beta = -0.047$ ,  $p < 0.001$ , Table 2,  
346 Fig. S2b). Male heterozygosity was not significantly associated with either grooming or  
347 proximity behavior.

348 Similar patterns were observed for females, although the effect of female rank was  
349 weaker than for male rank. Grooming and proximity were more likely to occur if the female in a  
350 dyad had more anubis ancestry (grooming:  $\beta = 0.513$ ,  $p < 0.001$ , Table 1, Fig. 1c; proximity:  $\beta =$   
351  $0.270$ ,  $p = 0.022$ , Table 2, Fig. S2c) and was higher ranking (grooming:  $\beta = -0.027$ ,  $p < 0.001$ ,  
352 Table 1, Fig. 1d; proximity:  $\beta = -0.024$ ,  $p < 0.001$ , Table 2, Fig. S2d). Female reproductive state,  
353 female age, transformed female age, and female heterozygosity did not significantly affect  
354 grooming or proximity behavior, nor did the interaction between female reproductive state and  
355 female genetic ancestry.

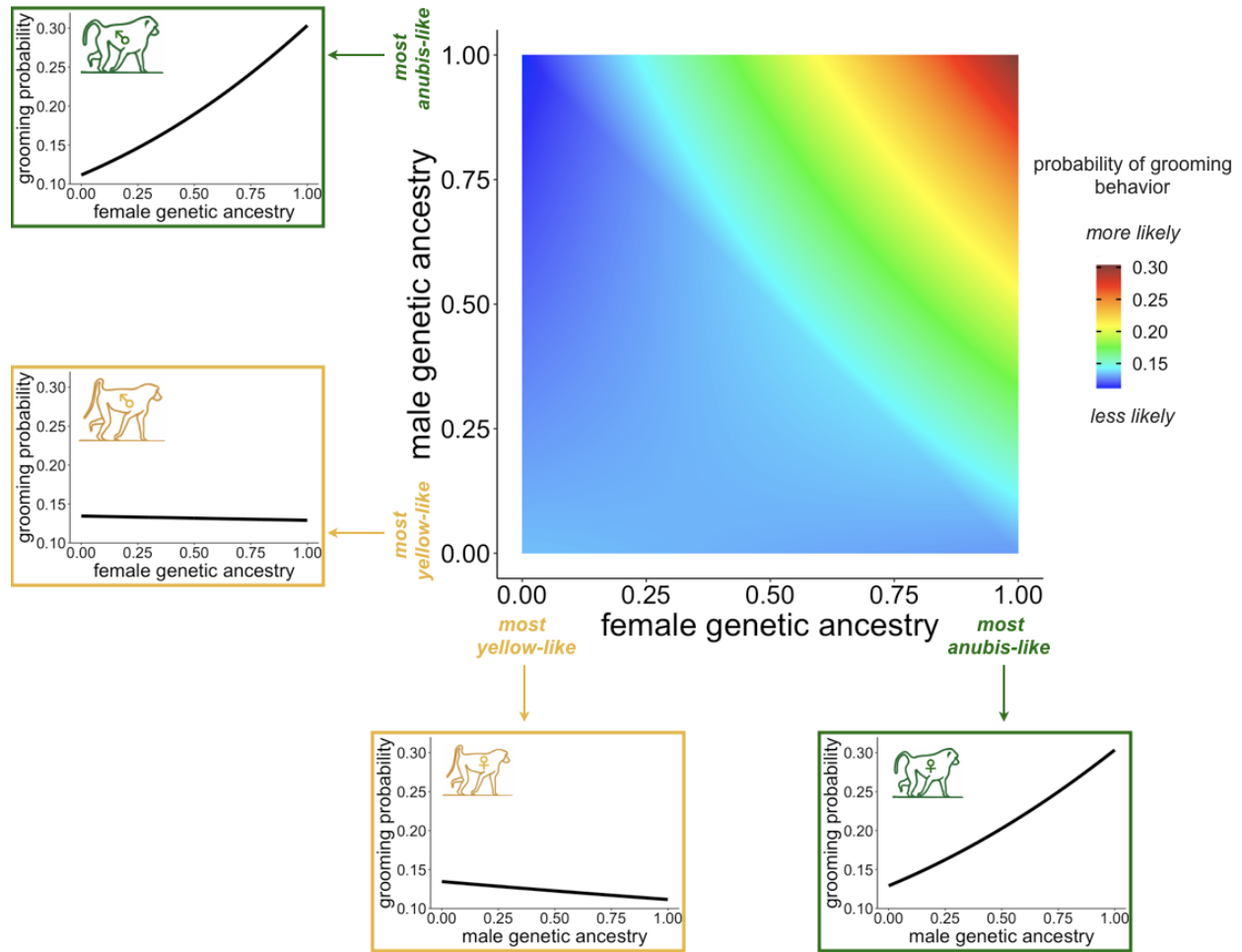


356 **Figure 1. Genetic ancestry and dominance rank predict the tendency to groom with an**  
357 **opposite-sex partner.** (a) The probability of grooming among co-resident opposite-sex pairs,  
358 per two-month interval, for the most anubis-like males (above the 90<sup>th</sup> percentile for male genetic  
359 ancestry in the data set, > 83.6% anubis ancestry, n=8 males) and the most yellow-like males  
360 (below the 10<sup>th</sup> percentile for male genetic ancestry in the data set, < 4.8% anubis ancestry, n=21  
361 males). Probabilities were calculated from the data without adjustment for other covariates. (b)  
362 The probability of grooming among co-resident opposite-sex pairs, per two-month interval, as a  
363 function of male dominance rank. Colored dots show probabilities based on counts of grooming  
364 occurrences, without adjustment for other covariates (as in (a)), and the dashed line shows the  
365 predicted relationship based on model estimates, assuming average values for all other covariates  
366 (see Supplementary Methods). Grey dots show the presence (y=1) or absence (y=0) of grooming  
367 behavior for all 17,356 female-male pair-interval combinations, as a function of male dominance  
368 rank (dots are jittered vertically for visibility). Non-integer values correspond to individuals that  
369 changed ranks during a two-month interval in the data set. (c) As in (a), for the most anubis-like  
370 females (above the 90<sup>th</sup> percentile for female genetic ancestry in the data set, > 76.0% anubis  
371 ancestry, n=11 females) and the most yellow-like females (below the 10<sup>th</sup> percentile for female  
372 genetic ancestry in the data set, < 3.5% anubis ancestry, n=10 females). (d) As in (b), with the  
373 probability of grooming shown as a function of female dominance rank.

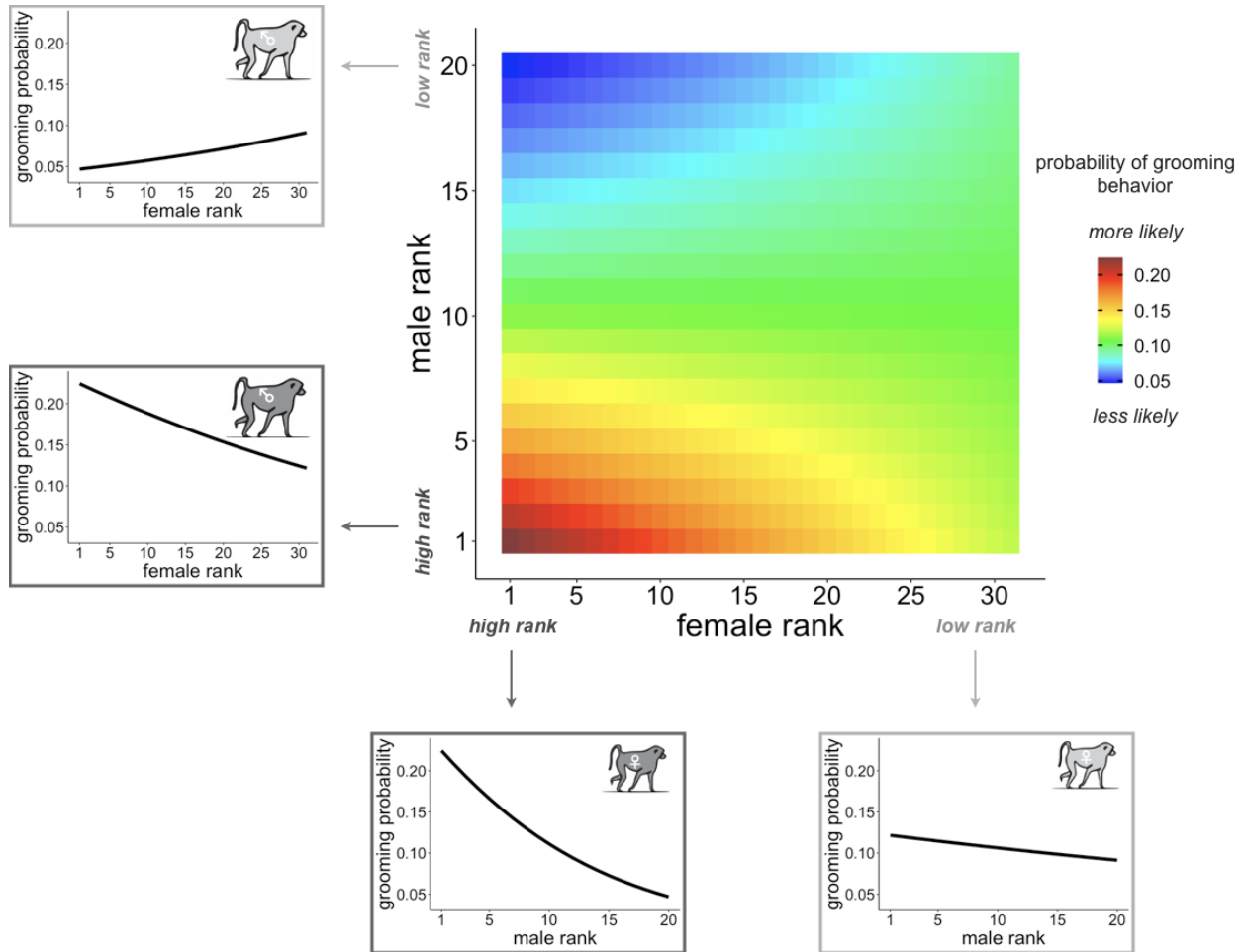
374 *Dyad-level characteristics: traits of both partners predict the propensity to affiliate with the*  
375 *opposite sex*

376 In addition to individual-level effects, we found that the combined characteristics of the  
377 female and male in each dyad predicted the probability of grooming and proximity. First,  
378 affiliative interactions were assortative with respect to genetic ancestry: they were more likely to  
379 occur when both partners were of similar genetic ancestry (i.e., both anubis-like or both yellow-  
380 like) and less likely to occur if they were of different genetic ancestry (grooming:  $\beta = 0.646$ ,  $p <$   
381  $0.001$ , Table 1, Fig. 2; proximity:  $\beta = 0.303$ ,  $p < 0.001$ , Table 2, Fig. S3). Overall, the probability  
382 of grooming and proximity was highest for pairs where both partners were anubis-like.  
383 Affiliative interactions were also assortative with respect to dominance rank: if both partners  
384 were high-ranking, the probability of affiliative interaction was higher than explained by the  
385 separate, additive effects of high male rank and high female rank alone (grooming:  $\beta = 0.003$ ,  $p$   
386  $< 0.001$ , Table 1, Fig. 3; proximity:  $\beta = 0.001$ ,  $p = 0.011$ , Table 2, Fig. S4). The effects of  
387 ancestry-based assortativity and rank-based assortativity are likely to be independent, as the  
388 assortative genetic ancestry index we used here is only weakly correlated with the product of  
389 male and female rank (the absolute value of Pearson's product-moment correlation:  $r < 0.07$ ,  $P <$   
390  $3.7 \times 10^{-13}$  for both grooming and proximity data sets). The correlation between rank and genetic  
391 ancestry is similarly weak within each sex (the absolute value of Pearson's product-moment  
392 correlation:  $r < 0.03$  for unique male rank-genetic ancestry combinations,  $P > 0.35$  for both  
393 grooming and proximity;  $r < 0.08$  for unique female rank-genetic ancestry combinations,  $P =$   
394  $0.37$  for grooming and  $P = 0.04$  for proximity).

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



402 **Figure 2. Combined genetic ancestry characteristics of females and males affect the**  
403 **probability of grooming.** The central heatmap shows the probability of grooming behavior as a  
404 function of female genetic ancestry (x-axis) and male genetic ancestry (y-axis), based on model  
405 estimates assuming average values for all other covariates (see Supplementary Methods).  
406 Assortative affiliative behavior is reflected by increased probability of yellow-like females  
407 grooming with yellow-like males, relative to anubis-like males, and anubis-like females  
408 grooming with anubis-like males, relative to yellow-like males. The probability of grooming is  
409 highest for pairs where both partners are anubis-like. Line graphs surrounding the heatmap show  
410 model predictions for the probability of grooming behavior for males (left) and females (bottom)  
411 at the two extremes of genetic ancestry, as a function of the genetic ancestry of potential  
412 opposite-sex social partners. Baboon illustrations adapted from Alberts and Altmann (2001).



413 **Figure 3. Combined rank characteristics of females and males affect the probability of**  
414 **grooming.** The central heatmap shows the probability of grooming behavior as a function of  
415 female dominance rank (x-axis) and male dominance rank (y-axis), based on model estimates  
416 assuming average values for all other covariates (see Supplementary Methods). The probability  
417 of grooming is highest for pairs where both partners are high ranking. Line graphs surrounding  
418 the heatmap show model predictions for the probability of grooming behavior for males (left)  
419 and females (bottom) at the extremes of the rank distribution, as a function of the dominance  
420 rank of potential opposite-sex social partners.

421 *Group demography influences grooming and proximity behavior, and observer effort affects*  
422 *ascertainment of these behaviors*

423 In addition to individual and dyadic-level effects, we found that aspects of group  
424 demography also influence male-female affiliative behavior. The probability of grooming was  
425 lower for all dyads when the social group contained more adult males ( $\beta = -0.030$ ,  $p = 0.018$ ,  
426 Table 1, Fig. S5a-b) and more adult females ( $\beta = -0.039$ ,  $p < 0.001$ , Table 1, Fig. S6a-b).  
427 Similarly, the probability of proximity was lower for all dyads when the social group contained  
428 more adult males ( $\beta = -0.036$ ,  $p = 0.005$ , Table 2, Fig. S5c-d), but not more adult females ( $\beta = -$   
429  $0.018$ ,  $p = 0.073$ , Table 2, Fig. S6c-d).

430 Finally, the probability of grooming and proximity behavior was higher for all dyads the  
 431 more days they were observed together in the same group (grooming:  $\beta = 0.047$ ,  $p < 0.001$ ,  
 432 Table 1; proximity:  $\beta = 0.037$ ,  $p < 0.001$ , Table 2). The probability of recording proximity  
 433 behavior, but not grooming behavior, also increased with greater observer effort (grooming:  $\beta =$   
 434  $0.002$ ,  $p = 0.425$ , Table 1; proximity:  $\beta = 0.027$ ,  $p < 0.001$ , Table 2).

**Table 1.** Results from a multivariate logistic regression model predicting grooming behavior.

Predictor variable <sup>a</sup>		Effect estimate	p-value <sup>b</sup>	Effect direction <sup>c</sup>
Intercept		-1.474	0.339	-
Genetic effects	<b>Female genetic ancestry</b>	<b>0.513</b>	<b>&lt;0.001</b>	<b>more anubis ancestry in females → ↑ Pr(groom)</b>
	<b>Male genetic ancestry</b>	<b>0.429</b>	<b>&lt;0.001</b>	<b>more anubis ancestry in males → ↑ Pr(groom)</b>
	<b>Assortative genetic ancestry index (<i>b</i>)</b>	<b>0.646</b>	<b>&lt;0.001</b>	<b>females and males of similar genetic ancestry → ↑ Pr(groom)</b>
	Female heterozygosity	-0.249	0.406	-
	Male heterozygosity	0.228	0.189	-
	Genetic relatedness	-0.090	0.489	-
Rank effects	<b>Female ordinal rank</b>	<b>-0.027</b>	<b>&lt;0.001</b>	<b>higher ranking females → ↑ Pr(groom)</b>
	<b>Male ordinal rank</b>	<b>-0.096</b>	<b>&lt;0.001</b>	<b>higher ranking males → ↑ Pr(groom)</b>
	<b>Female ordinal rank × male ordinal rank</b>	<b>0.003</b>	<b>&lt;0.001</b>	<b>females and males of similar rank → ↑ Pr(groom)</b>
Age effects	Female age ( $a_u$ )	-0.007	0.332	-
	Female age transformed ( $a_t$ )	-0.192	0.562	-
Demographic effects	<b>Adult females in group</b>	<b>-0.039</b>	<b>&lt;0.001</b>	<b>more adult females in group → ↓ Pr(groom)</b>
	<i>Adult males in group</i>	<i>-0.030</i>	<i>0.018</i>	<i>more adult males in group → ↓ Pr(groom)</i>
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	<b>Pair co-residency</b>	<b>0.047</b>	<b>&lt;0.001</b>	<b>longer co-residency → ↑ Pr(groom)</b>
Observer effects	Observer effort	0.002	0.425	-

<sup>a</sup> All variables included in this table were fit as fixed effects in the multivariate logistic regression model. Male and female identity were fit as random effects.

<sup>b</sup> Predictor variables for which  $p < 0.01$  are bolded and  $p < 0.05$  are italicized.

<sup>c</sup> Pr(groom) = probability of grooming.

**Table 2.** Results from a multivariate logistic regression model predicting proximity behavior.

Predictor variable <sup>a</sup>		Effect estimate	p-value <sup>b</sup>	Effect direction <sup>c</sup>
Intercept		-1.584	0.008	-
Genetic effects	<i>Female genetic ancestry</i>	<i>0.270</i>	<i>0.022</i>	<i>more anubis ancestry in females → ↑ Pr(prox)</i>
	<b>Male genetic ancestry</b>	<b>0.270</b>	<b>&lt;0.001</b>	<b>more anubis ancestry in males → ↑ Pr(prox)</b>
	<b>Assortative genetic ancestry index (b)</b>	<b>0.303</b>	<b>&lt;0.001</b>	<b>females and males of similar genetic ancestry → ↑ Pr(prox)</b>
	Female heterozygosity	-0.120	0.654	-
	Male heterozygosity	0.042	0.745	-
	Genetic relatedness	-0.041	0.693	-
Rank effects	<b>Female ordinal rank</b>	<b>-0.024</b>	<b>&lt;0.001</b>	<b>higher ranking females → ↑ Pr(prox)</b>
	<b>Male ordinal rank</b>	<b>-0.047</b>	<b>&lt;0.001</b>	<b>higher ranking males → ↑ Pr(prox)</b>
	<i>Female ordinal rank × male ordinal rank</i>	<i>0.001</i>	<i>0.011</i>	<i>females and males of similar rank → ↑ Pr(prox)</i>
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	-
	<b>Adult males in group</b>	<b>-0.036</b>	<b>0.005</b>	<b>more adult males in group → ↓ Pr(prox)</b>
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	<b>Pair co-residency</b>	<b>0.037</b>	<b>&lt;0.001</b>	<b>longer co-residency → ↑ Pr(prox)</b>
Observer effects	<b>Observer effort</b>	<b>0.027</b>	<b>&lt;0.001</b>	<b>greater observer effort → ↑ Pr(prox)</b>

<sup>a</sup> All variables included in this table were fit as fixed effects in the multivariate logistic regression model. Male and female identity were fit as random effects.

<sup>b</sup> Predictor variables for which  $p < 0.01$  are bolded and  $p < 0.05$  are italicized.

<sup>c</sup> Pr(prox) = probability of proximity.

## 435 DISCUSSION

436 Our results show that opposite-sex affiliative relationships are predicted by genetic  
437 ancestry in a natural baboon hybrid zone. Genetic ancestry effects are of particular interest  
438 because opposite-sex relationships must have a partial genetic basis in order to respond to natural  
439 selection. Additionally, genetic ancestry-associated differences provide *prima facie* evidence that  
440 this trait has evolved in the past. Specifically, in the Amboseli baboons, genetic ancestry acts  
441 alongside the effects of dominance rank and group demography to predict grooming and  
442 proximity behavior between adult males and adult females outside the mating context. These  
443 effects are not only detectable as a function of the individual characteristics of males and  
444 females, but also as a function of the properties of each opposite-sex pair. Although more anubis-  
445 like males and females were more likely to affiliate with the opposite sex regardless of their  
446 partner's ancestry, pairs of anubis-like males and anubis-like females were the most likely to be  
447 observed grooming or in close proximity (Figs. 2, S3). Our findings thus suggest that the  
448 tendency to engage in opposite-sex affiliative behavior partially diverged during baboon  
449 evolution to differentiate yellow and anubis baboons. We note that while we tested for the effects  
450 of genetic ancestry in this study, not genotype *per se*, baboons in Amboseli inherit anubis  
451 ancestry from both maternal and paternal lines (Tung et al., 2008). Our data set also contains  
452 many multigeneration hybrids, such that genetic ancestry estimates vary continuously between  
453 mostly yellow to mostly anubis. Thus, the signature of genetic ancestry reported here likely



454 arises from ancestry-associated differences in genotype, as opposed to ancestry-associated  
455 maternal or environmental effects on social preference.

456 These results add to previous evidence that male-female social bonds vary across baboon  
457 species (Baniel et al., 2016; Fischer et al., 2017; Goffe et al., 2016; Nguyen et al., 2009; Städele  
458 et al., 2019; Weingrill, 2000). For instance, male-female social relationships in chacma baboons  
459 are short-lived and occur primarily when females have dependent infants, whereas in Guinea  
460 baboons, close male-female social relationships commonly last for several years (Baniel et al.,  
461 2016; Fischer et al., 2017; Goffe et al., 2016). Yellow and anubis baboons, which have similar  
462 social organization and mating systems (multi-male, multi-female groups with female-biased  
463 dispersal and polygyny), are thought to fall between these two extremes, such that male-  
464 female relationships can sometimes, although not always, be long-lasting (Nguyen et al., 2009;  
465 Smuts, 1985; Städele et al., 2019). The identification of genetic ancestry effects in this study thus  
466 suggests that subtle differences in the nature of opposite-sex social relationships can evolve even  
467 between species that are otherwise quite similar in their social systems and behavioral  
468 repertoires. Identifying the molecular and neurochemical substrates for these differences,  
469 including whether they are shared with other taxa, is a fascinating topic for future work that  
470 could be facilitated by studies within natural hybrid zones.

471 Several lines of evidence also support the relevance of genetic ancestry effects on  
472 opposite-sex affiliative behavior to current variation in fitness. First, opposite-sex social  
473 relationships predict longevity in the Amboseli baboons (Archie et al., 2014; Campos et al.,  
474 2020), and longevity is an important contributor to lifetime reproductive success in both male  
475 and female baboons, as well as in other long-lived vertebrates (Alberts et al., 2006; Clutton-  
476 Brock, 1988; Lawler, 2007; McDonald, 1993; McLean et al., 2019; Newton, 1989; Wroblewski  
477 et al., 2009). Second, male-female social bonds can also lead to other reproductive gains,  
478 including offspring care that may improve survival (Anderson, 1992; Buchan et al., 2003; Busse  
479 & Hamilton, 1981; Huchard et al., 2013; Moscovice et al., 2009; Nguyen et al., 2009; Silk et al.,  
480 2020). Indeed, our findings that affiliative behavior was less common for any given dyad in large  
481 groups, and that both male and female rank predicted social interactions, suggest that male-  
482 female social bonds are an important and limited social resource for both sexes (Archie et al.,  
483 2014; Baniel et al., 2016; Haunhorst et al., 2019; Lemasson et al., 2008; Palombit et al., 2001;  
484 Seyfarth, 1976; Städele et al., 2019). This interpretation agrees with reports in chacma baboons  
485 that pregnant and lactating females direct aggression towards cycling females that are mate-  
486 guarded by and copulate with a shared male social partner (Baniel et al., 2018). Together with  
487 ancestry-related differences in affiliative behavior, our observations indicate that opposite-sex  
488 affiliative behavior has not only evolved in baboons in the past, but may also be the target of  
489 selection in the Amboseli population today.

490 The long-term ramifications of our findings for the stability or resolution of the hybrid  
491 zone remain somewhat unclear. If strong opposite-sex social bonds are fitness-enhancing, more  
492 anubis-like ancestry should be favored in Amboseli. However, assortative social preferences  
493 (both in mating and non-mating contexts) can also act as a barrier to admixture and could reduce  
494 the rate of anubis expansion. Along with previous findings in Amboseli (Charpentier et al., 2008;  
495 Franz et al., 2015; Tung et al., 2012), our results thus suggest that genetic ancestry is associated  
496 with a range of selectively relevant behavioral and life-history traits that do not universally point  
497 towards either anubis range expansion or to behaviorally-mediated reproductive isolation.  
498 Furthermore, any effect of genetic ancestry in baboons must necessarily be filtered through the  
499 effect of dominance rank, which is the most robust predictor of male mating behavior and, based

500 on the results of this study, also a major contributor to opposite-sex affiliative behavior (Tung et  
501 al., 2012). Finally, the effect of assortativity necessarily depends on the characteristics of  
502 available social partners. The interplay between genetic ancestry effects on an individual-level  
503 and at the dyadic-level will therefore be dynamic across populations and over time. The  
504 complexity of these co-acting factors may help explain why yellow baboons and anubis baboons  
505 remain phenotypically and genetically distinct, even though genomic analyses indicate repeated  
506 bouts of gene flow between yellow baboons and anubis baboons over hundreds to thousands of  
507 generations (Rogers et al., 2019; Wall et al., 2016). More broadly, our results suggest that simple  
508 behavioral barriers to admixture, such as wing pattern-based mate choice in butterflies or  
509 vibrational-based courtship signals in treehoppers (Jiggins et al., 2001; Rodríguez et al., 2004),  
510 are unlikely to occur in socially complex animals like baboons.

511 Finally, our study suggests both parallels and differences between opposite-sex social  
512 interactions within versus outside the context of mating. Several predictors of opposite-sex  
513 affiliation in this study overlap with predictors of mating behavior, including increased  
514 probability of both mating and social affiliation for higher-ranking and more anubis-like males,  
515 and assortativity based on both genetic ancestry and dominance rank (Tung et al., 2012).  
516 However, effects of female age and kinship were weak or undetectable in our analysis of male-  
517 female social bonds outside of the mating context. These results contrast with our previous result  
518 that male baboons are less likely to mate with females in older age classes (Tung et al., 2012),  
519 and with multiple lines of evidence that baboons and other primates avoid mating with relatives  
520 (Alberts & Altmann, 1995; Godoy et al., 2016; Packer, 1979a; Tung et al., 2012; Walker et al.,  
521 2017; Widdig et al., 2017). Because opposite-sex social affiliation is generally not a strong  
522 predictor of future mating events (although it may reflect a past history of mating: Huchard et al.,  
523 2010; Moscovice et al., 2010; Nguyen et al., 2009; Silk et al., 2020; Städele et al., 2019),  
524 differences in male-female behavior in mating versus non-mating contexts may arise because the  
525 benefits of opposite-sex social bonds differ from the benefits of mating. Alternatively or  
526 additionally, female choice and female-female competition may be more important in predicting  
527 grooming and proximity than mating behavior. Whereas only one or a few females experience  
528 estrus at any given time (Bercovitch, 1983; Bulger, 1993; Levy et al., 2020), all adult females are  
529 available as, and may actively be searching out, grooming partners. Notably, grooming  
530 relationships in baboons are more often initiated and maintained by females than by males,  
531 whereas males primarily absorb the costs of mate-guarding in a mating context (Alberts et al.,  
532 1996; Nguyen et al., 2009; Packer, 1979b; Palombit et al., 1997; but see Weyher et al., 2014).  
533 Thus, sexual and social preferences, and the extent to which they are expressed by males versus  
534 females, are likely to vary across different types of opposite-sex relationships—a distinction  
535 reminiscent of differences between social monogamy and genetic monogamy in pair-bonded  
536 birds and mammals (Carter & Perkeybile, 2018; Gowaty, 1996).

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561 **DATA STATEMENT**

562           Data on grooming behavior, proximity behavior, and all predictor variables tested in our  
563 models will be available on Dryad upon acceptance.

564 **REFERENCES**

- 565 Alberts, S. C. (2018). Social influences on survival and reproduction: Insights from a long-term  
566 study of wild baboons. *J Anim Ecol.* doi:10.1111/1365-2656.12887
- 567 Alberts, S. C., & Altmann, J. (1995). Balancing Costs and Opportunities: Dispersal in Male  
568 Baboons. *The American Naturalist*, 145(2), 279-306. doi:10.1086/285740
- 569 Alberts, S. C., & Altmann, J. (2001). Immigration and hybridization patterns of yellow and  
570 anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology*,  
571 53(4), 139-154. doi:DOI 10.1002/ajp.1
- 572 Alberts, S. C., & Altmann, J. (2012). The Amboseli Baboon Research Project: 40 Years of  
573 Continuity and Change. In P. M. Kappeler & D. P. Watts (Eds.), *Long-Term Field*  
574 *Studies of Primates* (pp. 261-287). Berlin Heidelberg: Springer-Verlag.
- 575 Alberts, S. C., Altmann, J., & Wilson, M. L. (1996). Mate guarding constrains foraging activity  
576 of male baboons. *Animal Behaviour*, 51, 1269-1277. doi:DOI 10.1006/anbe.1996.0131
- 577 Alberts, S. C., Archie, E. A., Altmann, J., & Tung, J. (2020). *Monitoring guide for the Amboseli*  
578 *Baboon Research Project: protocols for long-term monitoring and data collection.*  
579 Retrieved from  
580 [https://amboselibaboons.nd.edu/assets/384683/abrp\\_monitoring\\_guide\\_9april2020.pdf](https://amboselibaboons.nd.edu/assets/384683/abrp_monitoring_guide_9april2020.pdf)
- 581 Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: from  
582 mating opportunities to paternity success. *Animal Behaviour*, 72, 1177-1196.  
583 doi:10.1016/j.anbehav.2006.05.001
- 584 Alberts, S. C., Watts, H. E., & Altmann, J. (2003). Queuing and queue-jumping: long-term  
585 patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal*  
586 *Behaviour*, 65, 821-840. doi:10.1006/anbe.2003.2106
- 587 Anderson, C. M. (1986). Female age: Male preference and reproductive success in primates.  
588 *International Journal of Primatology*, 7(3), 305-326. doi:10.1007/bf02736394
- 589 Anderson, C. M. (1992). Male investment under changing conditions among chacma baboons at  
590 Suikerbosrand. *Am J Phys Anthropol*, 87(4), 479-496. doi:10.1002/ajpa.1330870408
- 591 Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation  
592 matters: both same-sex and opposite-sex relationships predict survival in wild female  
593 baboons. *Proc Biol Sci*, 281(1793). doi:10.1098/rspb.2014.1261
- 594 Baldassarre, D. T., & Webster, M. S. (2013). Experimental evidence that extra-pair mating  
595 drives asymmetrical introgression of a sexual trait. *Proc Biol Sci*, 280(1771), 20132175.  
596 doi:10.1098/rspb.2013.2175
- 597 Baldassarre, D. T., White, T. A., Karubian, J., & Webster, M. S. (2014). Genomic and  
598 morphological analysis of a semipermeable avian hybrid zone suggests asymmetrical  
599 introgression of a sexual signal. *Evolution*, 68(9), 2644-2657. doi:10.1111/evo.12457
- 600 Baniel, A., Cowlshaw, G., & Huchard, E. (2016). Stability and strength of male-female  
601 associations in a promiscuous primate society. *Behavioral Ecology and Sociobiology*,  
602 70(5), 761-775. doi:10.1007/s00265-016-2100-8
- 603 Baniel, A., Cowlshaw, G., & Huchard, E. (2018). Jealous females? Female competition and  
604 reproductive suppression in a wild promiscuous primate. *Proc Biol Sci*, 285(1886).  
605 doi:10.1098/rspb.2018.1332
- 606 Beehner, J. C., Onderdonk, D. A., Alberts, S. C., & Altmann, J. (2006). The ecology of  
607 conception and pregnancy failure in wild baboons. *Behavioral Ecology*, 17(5), 741-750.  
608 doi:10.1093/beheco/arl006

- 609 Bercovitch, F. B. (1983). Time Budgets and Consortships in Olive Baboons (*Papio-Anubis*).  
610 *Folia Primatologica*, 41(3-4), 180-190. doi:Doi 10.1159/000156130
- 611 Bergman, T. J., & Beehner, J. C. (2003). Hybrid zones and sexual selection: Insights from the  
612 Awash baboon hybrid zone (*Papio hamadryas anubis* x *P.h. hamadryas*). In C. B. Jones  
613 & American Society of Primatologists. (Eds.), *Sexual selection and reproductive*  
614 *competition in primates: new perspectives and directions* (pp. 503-537). Norman, Okla.:  
615 American Society of Primatologists.
- 616 Bergman, T. J., Phillips-Conroy, J. E., & Jolly, C. J. (2008). Behavioral variation and  
617 reproductive success of male baboons (*Papio anubis* x *Papio hamadryas*) in a hybrid  
618 social group. *Am J Primatol*, 70(2), 136-147. doi:10.1002/ajp.20467
- 619 Best, E. C., Dwyer, R. G., Seddon, J. M., & Goldizen, A. W. (2014). Associations are more  
620 strongly correlated with space use than kinship in female eastern grey kangaroos. *Animal*  
621 *Behaviour*, 89, 1-10. doi:10.1016/j.anbehav.2013.12.011
- 622 Black, J. M. (2001). Fitness consequences of long-term pair bonds in barnacle geese: monogamy  
623 in the extreme. *Behavioral Ecology*, 12(5), 640-645. doi:DOI 10.1093/beheco/12.5.640
- 624 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., . . .  
625 Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for  
626 Zero-inflated Generalized Linear Mixed Modeling. *R Journal*, 9(2), 378-400. doi:Doi  
627 10.32614/Rj-2017-066
- 628 Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male  
629 primate society. *Nature*, 425(6954), 179-181. doi:10.1038/nature01866
- 630 Bulger, J. B. (1993). Dominance Rank and Access To Estrous Females in Male Savanna  
631 Baboons. *Behaviour*, 127(1-2), 67-103. doi:10.1163/156853993x00434
- 632 Busse, C., & Hamilton, W. J., 3rd. (1981). Infant carrying by male chacma baboons. *Science*,  
633 212(4500), 1281-1283. doi:10.1126/science.212.4500.1281
- 634 Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated  
635 females increase reproductive success in feral horses. *Proc Natl Acad Sci U S A*, 106(33),  
636 13850-13853. doi:10.1073/pnas.0900639106
- 637 Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., & Alberts, S. C. (2020). Social  
638 bonds, social status and survival in wild baboons: a tale of two sexes. *Philos Trans R Soc*  
639 *Lond B Biol Sci*, 375(1811), 20190621. doi:10.1098/rstb.2019.0621
- 640 Carter, C. S., & Perkeybile, A. M. (2018). The Monogamy Paradox: What Do Love and Sex  
641 Have to Do With It? *Front Ecol Evol*, 6. doi:10.3389/fevo.2018.00202
- 642 Charpentier, M. J., Fontaine, M. C., Cherel, E., Renoult, J. P., Jenkins, T., Benoit, L., . . . Tung,  
643 J. (2012). Genetic structure in a dynamic baboon hybrid zone corroborates behavioural  
644 observations in a hybrid population. *Mol Ecol*, 21(3), 715-731. doi:10.1111/j.1365-  
645 294X.2011.05302.x
- 646 Charpentier, M. J., Tung, J., Altmann, J., & Alberts, S. C. (2008). Age at maturity in wild  
647 baboons: genetic, environmental and demographic influences. *Mol Ecol*, 17(8), 2026-  
648 2040. doi:10.1111/j.1365-294X.2008.03724.x
- 649 Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2012). Evidence for intra-sexual selection in wild  
650 female baboons. *Anim Behav*, 84(1), 21-27. doi:10.1016/j.anbehav.2012.03.010
- 651 Clutton-Brock, T. H. (1988). *Reproductive success: studies of individual variation in contrasting*  
652 *breeding systems*. Chicago: University of Chicago Press.
- 653 Cords, M. (1997). Friendships, alliances, reciprocity and repair *Machiavellian Intelligence II* (pp.  
654 24-49).

- 655 Cords, M. (2012). The behavior, ecology, and social evolution of cercopithecine monkeys. In J.  
656 C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of*  
657 *primate societies* (pp. 91-112). Chicago: The University of Chicago Press.
- 658 Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M. L., & Brent, L. J. N. (2019).  
659 Deconstructing sociality: the types of social connections that predict longevity in a group-  
660 living primate. *Proc Biol Sci*, 286(1917), 20191991. doi:10.1098/rspb.2019.1991
- 661 Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using  
662 multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, 164(4),  
663 1567-1587.
- 664 Fischer, E. K., Nowicki, J. P., & O'Connell, L. A. (2019a). Evolution of affiliation: patterns of  
665 convergence from genomes to behaviour. *Philosophical Transactions of the Royal*  
666 *Society B: Biological Sciences*, 374(1777). doi:10.1098/rstb.2018.0242
- 667 Fischer, J., Higham, J. P., Alberts, S. C., Barrett, L., Beehner, J. C., Bergman, T. J., . . . Zinner,  
668 D. (2019b). Insights into the evolution of social systems and species from baboon studies.  
669 *Elife*, 8. doi:10.7554/eLife.50989
- 670 Fischer, J., Kopp, G. H., Dal Pesco, F., Goffe, A., Hammerschmidt, K., Kalbitzer, U., . . . Zinner,  
671 D. (2017). Charting the neglected West: The social system of Guinea baboons. *Am J Phys*  
672 *Anthropol*, 162 Suppl 63, 15-31. doi:10.1002/ajpa.23144
- 673 Fitzpatrick, C. L., Altmann, J., & Alberts, S. C. (2014). Sources of variance in a female fertility  
674 signal: exaggerated estrous swellings in a natural population of baboons. *Behav Ecol*  
675 *Sociobiol*, 68(7), 1109-1122. doi:10.1007/s00265-014-1722-y
- 676 Franz, M., McLean, E., Tung, J., Altmann, J., & Alberts, S. C. (2015). Self-organizing  
677 dominance hierarchies in a wild primate population. *Proc Biol Sci*, 282(1814).  
678 doi:10.1098/rspb.2015.1512
- 679 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010a). Social  
680 and genetic interactions drive fitness variation in a free-living dolphin population. *Proc*  
681 *Natl Acad Sci U S A*, 107(46), 19949-19954. doi:10.1073/pnas.1007997107
- 682 Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., . . .  
683 Sherwin, W. B. (2010b). Home range overlap, matrilineal and biparental kinship drive  
684 female associations in bottlenose dolphins. *Animal Behaviour*, 80(3), 481-486.  
685 doi:10.1016/j.anbehav.2010.06.007
- 686 Gesquiere, L. R., Wango, E. O., Alberts, S. C., & Altmann, J. (2007). Mechanisms of sexual  
687 selection: sexual swellings and estrogen concentrations as fertility indicators and cues for  
688 male consort decisions in wild baboons. *Horm Behav*, 51(1), 114-125.  
689 doi:10.1016/j.yhbeh.2006.08.010
- 690 Godoy, I., Vigilant, L., & Perry, S. E. (2016). Inbreeding risk, avoidance and costs in a group-  
691 living primate, *Cebus capucinus*. *Behavioral Ecology and Sociobiology*, 70(9), 1601-  
692 1611. doi:10.1007/s00265-016-2168-1
- 693 Goffe, A. S., Zinner, D., & Fischer, J. (2016). Sex and friendship in a multilevel society:  
694 behavioural patterns and associations between female and male Guinea baboons. *Behav*  
695 *Ecol Sociobiol*, 70, 323-336. doi:10.1007/s00265-015-2050-6
- 696 Gowaty, P. A. (1996). Battle of the sexes and origins of monogamy. In J. M. Black (Ed.),  
697 *Partnerships in birds: the study of monogamy* (pp. 21-52). Oxford: Oxford University  
698 Press.

- 699 Griggio, M., & Hoi, H. (2011). An experiment on the function of the long-term pair bond period  
700 in the socially monogamous bearded reedling. *Animal Behaviour*, *82*(6), 1329-1335.  
701 doi:10.1016/j.anbehav.2011.09.016
- 702 Haunhorst, C. B., Fürtbauer, I., Schülke, O., & Ostner, J. (2019). Female macaques compete for  
703 'power' and 'commitment' in their male partners. *Evolution and Human Behavior*.  
704 doi:10.1016/j.evolhumbehav.2019.11.001
- 705 Haunhorst, C. B., Heesen, M., Ostner, J., & Schülke, O. (2017). Social bonds with males lower  
706 the costs of competition for wild female Assamese macaques. *Animal Behaviour*, *125*,  
707 51-60. doi:10.1016/j.anbehav.2017.01.008
- 708 Hewitt, G. M. (1988). Hybrid zones-natural laboratories for evolutionary studies. *Trends Ecol*  
709 *Evol*, *3*(7), 158-167. doi:10.1016/0169-5347(88)90033-X
- 710 Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlshaw, G., & Raymond, M. (2010).  
711 More than friends? Behavioural and genetic aspects of heterosexual associations in wild  
712 chacma baboons. *Behavioral Ecology and Sociobiology*, *64*(5), 769-781.  
713 doi:10.1007/s00265-009-0894-3
- 714 Huchard, E., Charpentier, M. J., Marshall, H., King, A. J., Knapp, L. A., & Cowlshaw, G.  
715 (2013). Paternal effects on access to resources in a promiscuous primate society.  
716 *Behavioral Ecology*, *24*(1), 229-236. doi:10.1093/beheco/ars158
- 717 Insel, T. R., & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization  
718 in monogamous and polygamous voles. *Proceedings of the National Academy of*  
719 *Sciences*, *89*(13), 5981-5985. doi:10.1073/pnas.89.13.5981
- 720 Insel, T. R., Wang, Z. X., & Ferris, C. F. (1994). Patterns of brain vasopressin receptor  
721 distribution associated with social organization in microtine rodents. *The Journal of*  
722 *Neuroscience*, *14*(9), 5381-5392. doi:10.1523/jneurosci.14-09-05381.1994
- 723 Jiggins, C. D., Naisbit, R. E., Coe, R. L., & Mallet, J. (2001). Reproductive isolation caused by  
724 colour pattern mimicry. *Nature*, *411*(6835), 302-305. doi:10.1038/35077075
- 725 Johnson, Z. V., & Young, L. J. (2015). Neurobiological mechanisms of social attachment and  
726 pair bonding. *Curr Opin Behav Sci*, *3*, 38-44. doi:10.1016/j.cobeha.2015.01.009
- 727 Kempenaers, B. (2007). Mate Choice and Genetic Quality: A Review of the Heterozygosity  
728 Theory *Advances in the Study of Behavior* (Vol. 37, pp. 189-278).
- 729 Kronforst, M. R., Young, L. G., Kapan, D. D., McNeely, C., O'Neill, R. J., & Gilbert, L. E.  
730 (2006). Linkage of butterfly mate preference and wing color preference cue at the  
731 genomic location of *wingless*. *Proceedings of the National Academy of Sciences of the*  
732 *United States of America*, *103*(17), 6575-6580. doi:10.1073/pnas.0509685103
- 733 Kulik, L., Muniz, L., Mundry, R., & Widdig, A. (2012). Patterns of interventions and the effect  
734 of coalitions and sociality on male fitness. *Mol Ecol*, *21*(3), 699-714. doi:10.1111/j.1365-  
735 294X.2011.05250.x
- 736 Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female  
737 chimpanzees (*Pan troglodytes*). *Am J Primatol*, *71*(10), 840-851. doi:10.1002/ajp.20711
- 738 Lawler, R. R. (2007). Fitness and extra-group reproduction in male Verreaux's sifaka: An  
739 analysis of reproductive success from 1989-1999. *Am J Phys Anthropol*, *132*(2), 267-277.  
740 doi:10.1002/ajpa.20507
- 741 Lea, A. J., Altmann, J., Alberts, S. C., & Tung, J. (2015). Developmental constraints in a wild  
742 primate. *Am Nat*, *185*(6), 809-821. doi:10.1086/681016
- 743 Lemasson, A., Palombit, R. A., & Jubin, R. (2008). Friendships between males and lactating  
744 females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence



- 745 from playback experiments. *Behavioral Ecology and Sociobiology*, 62(6), 1027-1035.  
746 doi:10.1007/s00265-007-0530-z
- 747 Levy, E. J., Zippel, M. N., McLean, E., Campos, F. A., Dasari, M., Fogel, A. S., . . . Archie, E.  
748 A. (2020). A comparison of dominance rank metrics reveals multiple competitive  
749 landscapes in an animal society. *Proc Biol Sci*, 287(1934), 20201013.  
750 doi:10.1098/rspb.2020.1013
- 751 Mavárez, J., Salazar, C. A., Bermingham, E., Salcedo, C., Jiggins, C. D., & Linares, M. (2006).  
752 Speciation by hybridization in *Heliconius* butterflies. *Nature*, 441(7095), 868-871.  
753 doi:10.1038/nature04738
- 754 McDonald, D. B. (1993). Demographic consequences of sexual selection in the long-tailed  
755 manakin. *Behavioral Ecology*, 4(4), 297-309. doi:DOI 10.1093/beheco/4.4.297
- 756 McLean, E. M., Archie, E. A., & Alberts, S. C. (2019). Lifetime Fitness in Wild Female  
757 Baboons: Trade-Offs and Individual Heterogeneity in Quality. *Am Nat*, 194(6), 745-759.  
758 doi:10.1086/705810
- 759 Ménard, N., von Segesser, F., Scheffrahn, W., Pastorini, J., Vallet, D., Gaci, B., . . . Gautier-  
760 Hion, A. (2001). Is male-infant caretaking related to paternity and/or mating activities in  
761 wild Barbary macaques (*Macaca sylvanus*)? *Comptes Rendus de l'Académie des Sciences*  
762 - *Series III - Sciences de la Vie*, 324(7), 601-610. doi:[https://doi.org/10.1016/S0764-](https://doi.org/10.1016/S0764-4469(01)01339-7)  
763 4469(01)01339-7
- 764 Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal*  
765 *Behaviour*, 77(3), 633-640. doi:10.1016/j.anbehav.2008.11.021
- 766 Möller, L. M., Beheregaray, L. B., Harcourt, R. G., & Krutzen, M. (2001). Alliance membership  
767 and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern  
768 Australia. *Proc Biol Sci*, 268(1479), 1941-1947. doi:10.1098/rspb.2001.1756
- 769 Moscovice, L. R., Di Fiore, A., Crockford, C., Kitchen, D. M., Wittig, R., Seyfarth, R. M., &  
770 Cheney, D. L. (2010). Hedging their bets? Male and female chacma baboons form  
771 friendships based on likelihood of paternity. *Animal Behaviour*, 79(5), 1007-1015.  
772 doi:10.1016/j.anbehav.2010.01.013
- 773 Moscovice, L. R., Heesen, M., Di Fiore, A., Seyfarth, R. M., & Cheney, D. L. (2009). Paternity  
774 alone does not predict long-term investment in juveniles by male baboons. *Behav Ecol*  
775 *Sociobiol*, 63(10), 1471-1482. doi:10.1007/s00265-009-0781-y
- 776 Newton, I. (1989). *Lifetime reproduction in birds*. London ; San Diego: Academic.
- 777 Nguyen, N., Van Horn, R. C., Alberts, S. C., & Altmann, J. (2009). "Friendships" between new  
778 mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio*  
779 *cynocephalus*). *Behav Ecol Sociobiol*, 63(9), 1331-1344. doi:10.1007/s00265-009-0786-6
- 780 Okello, M. M., Kenana, L., Maliti, H., Kiringe, J. W., Kanga, E., Warinwa, F., . . . Mwangi, P.  
781 (2016). Population density of elephants and other key large herbivores in the Amboseli  
782 ecosystem of Kenya in relation to droughts. *Journal of Arid Environments*, 135, 64-74.  
783 doi:10.1016/j.jaridenv.2016.08.012
- 784 Packer, C. (1979a). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal*  
785 *Behaviour*, 27(1), 1-36. doi:10.1016/0003-3472(79)90126-x
- 786 Packer, C. (1979b). Male dominance and reproductive activity in *Papio anubis*. *Animal*  
787 *Behaviour*, 27(Feb), 37-45. doi:Doi 10.1016/0003-3472(79)90127-1
- 788 Palombit, R. A., Cheney, D. L., & Seyfarth, R. M. (2001). Female–female competition for male  
789 ‘friends’ in wild chacma baboons (*Papio cynocephalus ursinus*). *Animal Behaviour*,  
790 61(6), 1159-1171. doi:10.1006/anbe.2000.1690

- 791 Palombit, R. A., Seyfarth, R. M., & Cheney, D. L. (1997). The adaptive value of 'friendships' to  
792 female baboons: experimental and observational evidence. *Animal Behaviour*, *54*, 599-  
793 614.
- 794 Pew, J., Wang, J., Muir, P., & Frasier, T. (2015). related: an R package for analyzing pairwise  
795 relatedness data based on codominant molecular markers (Version R package version  
796 1.0).
- 797 Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using  
798 multilocus genotype data. *Genetics*, *155*(2), 945-959.
- 799 Queller, D. C., & Goodnight, K. F. (1989). Estimating Relatedness Using Genetic-Markers.  
800 *Evolution*, *43*(2), 258-275. doi:Doi 10.2307/2409206
- 801 R Core Team. (2019). R: A language and environment for statistical computing. Vienna, Austria:  
802 R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- 803 Ribble, D. O. (1992). Lifetime Reproductive Success and Its Correlates in the Monogamous  
804 Rodent, *Peromyscus-Californicus*. *Journal of Animal Ecology*, *61*(2), 457-468. doi:Doi  
805 10.2307/5336
- 806 Rodríguez, R. L., Sullivan, L. E., & Crocft, R. B. (2004). Vibrational Communication and  
807 Reproductive Isolation in the *Enchenopa Binotata* Species Complex of Treehoppers  
808 (Hemiptera: Membracidae). *Evolution*, *58*(3), 571-578. doi:10.1111/j.0014-  
809 3820.2004.tb01679.x
- 810 Rogers, J., Raveendran, M., Harris, R. A., Mailund, T., Leppala, K., Athanasiadis, G., . . .  
811 Baboon Genome Analysis, C. (2019). The comparative genomics and complex  
812 population history of *Papio* baboons. *Sci Adv*, *5*(1), eaau6947.  
813 doi:10.1126/sciadv.aau6947
- 814 Rosenbaum, S., Maldonado-Chaparro, A. A., & Stoinski, T. S. (2016). Group structure predicts  
815 variation in proximity relationships between male-female and male-infant pairs of  
816 mountain gorillas (*Gorilla beringei beringei*). *Primates*, *57*(1), 17-28.  
817 doi:10.1007/s10329-015-0490-2
- 818 Sadino, J. M., & Donaldson, Z. R. (2018). Prairie Voles as a Model for Understanding the  
819 Genetic and Epigenetic Regulation of Attachment Behaviors. *ACS Chem Neurosci*, *9*(8),  
820 1939-1950. doi:10.1021/acchemneuro.7b00475
- 821 Samuels, A., & Altmann, J. (1986). Immigration of a *Papio anubis* male into a group of *Papio*  
822 *cynocephalus* baboons and evidence for an *anubis-cynocephalus* hybrid zone in  
823 Amboseli, Kenya. *International Journal of Primatology*, *7*(2), 131-138.
- 824 Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: pair bond  
825 duration increases individual fitness independent of age-related variation. *Proc Biol Sci*,  
826 *281*(1786). doi:10.1098/rspb.2013.2843
- 827 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance  
828 reproductive success in male macaques. *Curr Biol*, *20*(24), 2207-2210.  
829 doi:10.1016/j.cub.2010.10.058
- 830 Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour*,  
831 *24*(4), 917-938. doi:10.1016/s0003-3472(76)80022-x
- 832 Seyfarth, R. M. (1978). Social relationships among adult male and female baboons. II. Behaviour  
833 throughout the female reproductive cycle. *Behaviour*, *64*, 227-247.
- 834 Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2014). Social bonds in female baboons: the  
835 interaction between personality, kinship and rank. *Animal Behaviour*, *87*, 23-29.  
836 doi:10.1016/j.anbehav.2013.10.008

- 837 Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social relationships.  
838 *Evol Anthropol*, 22(5), 213-225. doi:10.1002/evan.21367
- 839 Silk, J. B., Alberts, S. C., & Altmann, J. (2006a). Social relationships among adult female  
840 baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds.  
841 *Behavioral Ecology and Sociobiology*, 61(2), 197-204. doi:10.1007/s00265-006-0250-9
- 842 Silk, J. B., Altmann, J., & Alberts, S. C. (2006b). Social relationships among adult female  
843 baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral*  
844 *Ecology and Sociobiology*, 61(2), 183-195. doi:10.1007/s00265-006-0249-2
- 845 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . .  
846 Cheney, D. L. (2009). The benefits of social capital: close social bonds among female  
847 baboons enhance offspring survival. *Proc Biol Sci*, 276(1670), 3099-3104.  
848 doi:10.1098/rspb.2009.0681
- 849 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . .  
850 Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female  
851 baboons. *Curr Biol*, 20(15), 1359-1361. doi:10.1016/j.cub.2010.05.067
- 852 Silk, J. B., Städele, V., Roberts, E. K., Vigilant, L., & Strum, S. C. (2020). Shifts in Male  
853 Reproductive Tactics over the Life Course in a Polygynandrous Mammal. *Current*  
854 *Biology*. doi:10.1016/j.cub.2020.02.013
- 855 Smeltzer, M. D., Curtis, J. T., Aragona, B. J., & Wang, Z. (2006). Dopamine, oxytocin, and  
856 vasopressin receptor binding in the medial prefrontal cortex of monogamous and  
857 promiscuous voles. *Neurosci Lett*, 394(2), 146-151. doi:10.1016/j.neulet.2005.10.019
- 858 Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2006). Rank-related partner choice in the  
859 fission–fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and*  
860 *Sociobiology*, 61(5), 753-765. doi:10.1007/s00265-006-0305-y
- 861 Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine Pub. Co.
- 862 Städele, V., Roberts, E. R., Barrett, B. J., Strum, S. C., Vigilant, L., & Silk, J. B. (2019). Male–  
863 female relationships in olive baboons (*Papio anubis*): Parenting or mating effort? *Journal*  
864 *of Human Evolution*, 127, 81-92. doi:10.1016/j.jhevol.2018.09.003
- 865 Tung, J., Charpentier, M. J., Garfield, D. A., Altmann, J., & Alberts, S. C. (2008). Genetic  
866 evidence reveals temporal change in hybridization patterns in a wild baboon population.  
867 *Mol Ecol*, 17(8), 1998-2011. doi:10.1111/j.1365-294X.2008.03723.x
- 868 Tung, J., Charpentier, M. J., Mukherjee, S., Altmann, J., & Alberts, S. C. (2012). Genetic effects  
869 on mating success and partner choice in a social mammal. *Am Nat*, 180(1), 113-129.  
870 doi:10.1086/665993
- 871 Tuqa, J. H., Funston, P., Musyoki, C., Ojwang, G. O., Gichuki, N. N., Bauer, H., . . . de Iongh,  
872 H. H. (2014). Impact of severe climate variability on lion home range and movement  
873 patterns in the Amboseli ecosystem, Kenya. *Global Ecology and Conservation*, 2, 1-10.  
874 doi:10.1016/j.gecco.2014.07.006
- 875 van Schaik, C. P., & Paul, A. (1996). Male care in primates: does it ever reflect paternity?  
876 *Evolutionary Anthropology*, 5, 152-156.
- 877 Walker, K. K., Rudicell, R. S., Li, Y., Hahn, B. H., Wroblewski, E., & Pusey, A. E. (2017).  
878 Chimpanzees breed with genetically dissimilar mates. *R Soc Open Sci*, 4(1), 160422.  
879 doi:10.1098/rsos.160422
- 880 Wall, J. D., Schlebusch, S. A., Alberts, S. C., Cox, L. A., Snyder-Mackler, N., Nevenon, K.  
881 A., . . . Tung, J. (2016). Genomewide ancestry and divergence patterns from low-

- 882 coverage sequencing data reveal a complex history of admixture in wild baboons. *Mol*  
883 *Ecol*, 25(14), 3469-3483. doi:10.1111/mec.13684
- 884 Wang, J. (2011). COANCESTRY: a program for simulating, estimating and analysing  
885 relatedness and inbreeding coefficients. *Mol Ecol Resour*, 11(1), 141-145.  
886 doi:10.1111/j.1755-0998.2010.02885.x
- 887 Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: fitness  
888 consequences of social partner choice in female house mice. *Animal Behaviour*, 75(3),  
889 801-808. doi:10.1016/j.anbehav.2007.06.017
- 890 Weingrill, T. (2000). Infanticide and the Value of Male-Female Relationships in Mountain  
891 Chacma Baboons. *Behaviour*, 137(3), 337-359. doi:10.1163/156853900502114
- 892 Weyher, A. H., Phillips-Conroy, J. E., Fourrier, M. S., & Jolly, C. J. (2014). Male-driven  
893 grooming bouts in mixed-sex dyads of Kinda baboons (*Papio kindae*). *Folia*  
894 *Primatologica*, 85(3), 178-191. doi:10.1159/000362544
- 895 Whitten, P. L. (1987). Infants and adult males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R.  
896 W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 343-357). Chicago: The  
897 University of Chicago Press.
- 898 Widdig, A., Muniz, L., Minkner, M., Barth, Y., Bley, S., Ruiz-Lambides, A., . . . Kulik, L.  
899 (2017). Low incidence of inbreeding in a long-lived primate population isolated for 75  
900 years. *Behav Ecol Sociobiol*, 71(1), 18. doi:10.1007/s00265-016-2236-6
- 901 Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal  
902 relatedness and age proximity regulate social relationships among adult female rhesus  
903 macaques. *Proc Natl Acad Sci U S A*, 98(24), 13769-13773. doi:10.1073/pnas.241210198
- 904 Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., &  
905 Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan*  
906 *trogodytes schweinfurthii*. *Anim Behav*, 77(4), 873-885.  
907 doi:10.1016/j.anbehav.2008.12.014
- 908 Young, K. A., Gobrogge, K. L., Liu, Y., & Wang, Z. (2011). The neurobiology of pair bonding:  
909 insights from a socially monogamous rodent. *Front Neuroendocrinol*, 32(1), 53-69.  
910 doi:10.1016/j.yfrne.2010.07.006
- 911 Young, L. J., Huot, B., Nilsen, R., Wang, Z., & Insel, T. R. (1996). Species differences in central  
912 oxytocin receptor gene expression: comparative analysis of promoter sequences. *J*  
913 *Neuroendocrinol*, 8(10), 777-783. doi:10.1046/j.1365-2826.1996.05188.x
- 914 Young, L. J., Nilsen, R., Waymire, K. G., MacGregor, G. R., & Insel, T. R. (1999). Increased  
915 affiliative response to vasopressin in mice expressing the V<sub>1a</sub> receptor from a  
916 monogamous vole. *Nature*, 400(6746), 766-768. doi:10.1038/23475
- 917 Young, L. J., Waymire, K. G., Nilsen, R., Macgregor, G. R., Wang, Z., & Insel, T. R. (1997a).  
918 The 5' flanking region of the monogamous prairie vole oxytocin receptor gene directs  
919 tissue-specific expression in transgenic mice. *Ann N Y Acad Sci*, 807, 514-517.  
920 doi:10.1111/j.1749-6632.1997.tb51955.x
- 921 Young, L. J., Winslow, J. T., Nilsen, R., & Insel, T. R. (1997b). Species differences in V<sub>1a</sub>  
922 receptor gene expression in monogamous and nonmonogamous voles: Behavioral  
923 consequences. *Behavioral Neuroscience*, 111(3), 599-605. doi:10.1037//0735-  
924 7044.111.3.599
- 925 Young, R. L., Ferkin, M. H., Ockendon-Powell, N. F., Orr, V. N., Phelps, S. M., Pogany, A., . . .  
926 Hofmann, H. A. (2019). Conserved transcriptomic profiles underpin monogamy across  
927 vertebrates. *Proc Natl Acad Sci U S A*, 116(4), 1331-1336. doi:10.1073/pnas.1813775116