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Genetic variance and indirect genetic effects for affiliative social behavior in a wild primate

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1 **Title: Genetic variance and indirect genetic effects for affiliative social behavior in a wild primate.**

2 **Running title: Genetic variance for social behavior**

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4
5 **ABSTRACT**

6 Affiliative social behaviors are linked to fitness components in multiple species. However, the role of
7 genetic variance in shaping such behaviors remains largely unknown, limiting our understanding of how
8 affiliative behaviors can respond to natural selection. Here, we employed the ‘animal model’ to estimate
9 environmental and genetic sources of variance and covariance in grooming behavior in the well-studied
10 Amboseli wild baboon population. We found that the tendency for a female baboon to groom others
11 (‘grooming given’) is heritable ($h^2=0.22\pm 0.048$), and that several environmental variables – including
12 dominance rank and the availability of kin as grooming partners – contribute to variance in this
13 grooming behavior. We also detected small but measurable variance due to the indirect genetic effect
14 of partner identity on the amount of grooming given within dyadic grooming partnerships. The indirect
15 and direct genetic effects for grooming given were positively correlated ($r=0.74\pm 0.09$). Our results
16 provide insight into the evolvability of affiliative behavior in wild animals, including the possibility for
17 correlations between direct and indirect genetic effects to accelerate the response to selection. As such
18 they provide novel information about the genetic architecture of social behavior in nature, with
19 important implications for the evolution of cooperation and reciprocity.

20
21
22 **INTRODUCTION**

23 Social relationships, often measured by the frequency and intensity of social interactions with others,
24 are linked to individual survival or reproductive success in humans and a number of social mammals
25 (e.g., Holt-Lunstad et al. 2010; Stanton and Mann 2012; McFarland and Majolo 2013; Vander Wal et al.
26 2015; Ellis et al. 2017; Thompson and Cords 2018, Cameron et al. 2009; Schülke et al. 2010, Feldblum et
27 al. 2021). These effects may arise, in part, because affiliative social interactions – i.e., interactions that
28 are primarily positive, such as grooming in primates – confer several potential benefits, including
29 parasite removal (Ezenwa et al. 2016), access to mating opportunities (Diaz-Muñoz et al. 2014),
30 decreased intra-group conflict (Silk 2002) and enhanced success in within and between group
31 competitive encounters (Wrangham 1980).

32 Given the links between affiliative social interactions and fitness-related traits in highly social
33 species, natural selection probably favors individuals who are more affiliative with conspecifics.
34 However, despite the clear and compelling links between affiliative social behavior and fitness-related
35 traits, we have a limited understanding of how affiliative social behavior evolves. Addressing this
36 question requires understanding the genetic architecture of highly social traits, as well as determining
37 the relative contributions of genetic and environmental variation to phenotypic variation in wild
38 populations where natural selection is acting. Specifically, for an evolutionary response to selection to
39 occur, phenotypic variation in affiliative social behavior must have an underlying heritable component.

40 Furthermore, when a trait is affected by interactions between individuals, its genetic architecture is
41 determined not only by the focal individual’s own genotype (i.e., direct genetic effects, or DGEs) but by
42 the genotype of its partner(s) (i.e. indirect genetic effects, or IGEs; (reviewed in Moore et al. 1997,

43 McGlothlin et al. 2010, Baud et al. 2022)). Some of the most well-documented examples of IGEs occur
44 between mothers and offspring (e.g., maternal genetic effects), which occur when the offspring's
45 phenotype is influenced by the genotype of its mother, independently of the direct effects of the genes
46 the offspring inherits. For example, maternal genotype explains 11% of the variance in offspring birth
47 weight in a feral population of Soay sheep (Wilson et al. 2005) and 31% of the variance in birth weight in
48 red deer (Gauzere et al. 2020). Indirect genetic effects between unrelated partners can also be
49 substantial: in a study of Eastern chipmunks, 23% of the variance in fecundity and 36% of the variance in
50 'trappability' (the number of times captured) were explained by IGEs (Santostefano et al. 2021).

51 Importantly, the magnitude of indirect genetic effects and their genetic relationship to direct genetic
52 effects can fundamentally alter our expectation for how traits will evolve. For example, Wilson et al.
53 (2009) found a positive genetic correlation between DGEs and IGEs for some aggressive phenotypes in a
54 lab population of deer mice, implying that the same genotypes that promote aggression in the bearer
55 also promote aggression in those with whom it interacts. Selection for increased aggression, then,
56 would result in evolution of the social environment as well as a change in the frequency of 'aggressive
57 alleles': each successive generation would experience a more aggressive social environment than that
58 of their parents (even the individuals who themselves did not carry 'aggressive alleles') and hence would
59 themselves be more aggressive. That is, phenotypic evolution would be greater than expected if DGEs
60 and IGEs were independent (for a fuller treatment of the quantitative genetic approach to
61 understanding indirect genetic effects, see Moore et al. 1997; Wolf et al. 1998; Hunt and Simmons 2002;
62 Bijma and Wade 2008 and references therein).

63 The recognized importance of IGEs has motivated the development of two approaches to studying
64 them (reviewed in Wolf et al. 1998, McGlothlin & Brodie 2009). The "trait-based" approach involves
65 treating specific, measured traits in conspecifics as a component of the environment that affects the
66 phenotype of the focal individual, and then estimating the strength and direction of that effect (e.g.,
67 Moore et al. 1997, Bleakley & Brodie 2009, Fisher 2023). The other approach is based on variance
68 partitioning, which estimates the contributions of random and fixed effects to variance in the trait by
69 incorporating pedigree (i.e., genetic) information into random effects estimates and modeling
70 environmental variables as fixed effects in a mixed effects linear model, often called the 'animal model'
71 (e.g., Wilson et al. 2009, Houslay et al. 2021, Godoy et al. 2022). The two approaches have different
72 advantages, and their results are largely compatible (McGlothlin & Brodie 2009). Here, we take the
73 variance-partitioning approach.

74 Given the importance of indirect genetic effects for understanding the genetic components of social
75 behavior – which, by definition, is influenced by genetic contributions of multiple individuals –
76 researchers have increasingly turned their attention towards understanding the genetic architecture of
77 social behaviors in both wild and captive populations. While much progress has been made towards
78 understanding the genetic basis of competitive interactions (e.g., Edwards et al. 2006, Wilson et al.
79 2011, Sartori and Mantovani 2012, Saltz 2013), much less is known about the quantitative genetics of
80 affiliative social behaviors among wild animals, and especially about the role of IGEs in the genetic
81 architecture of these traits. For instance, two studies have investigated the heritability and/or genetic
82 architecture of spatial affiliation (maintaining close proximity to conspecifics) in non-human primates,
83 reporting modest heritability for this trait (Blomquist and Brent 2014 and Godoy et al. 2022), although
84 neither study investigated the role of IGEs in this behavior. Other studies have focused on less direct

85 measures of affiliative social behavior such as social network metrics (e.g., Fowler et al. 2009; Lea et al.
86 2010; Brent et al. 2013) or cooperative behaviors (e.g., Bleakley and Brodie 2009, Kasper et al. 2017,
87 Houslay et al. 2021). These findings are also consistent with evidence from human populations
88 suggesting that loneliness and social integration are weakly to modestly heritable and subject to strong
89 environmental effects, including IGEs (Day et al. 2018, Abdellaoui et al. 2019). IGEs for cooperative
90 antipredator behavior have been documented laboratory guppies (Bleakley and Brodie 2009), for social
91 network metrics in flies (Wice and Saltz 2023) and for maternal-offspring interactions in mice (Ashbrook
92 et al. 2015). However, the presence and magnitude of IGEs for affiliative social behaviors remains
93 largely unexplored in wild animals. This represents a critical gap in our understanding of the genetic
94 architecture of affiliative social behaviors and limits our ability to understand how affiliative social
95 relationships evolve.

96 Here, we contribute to filling this gap by combining detailed, long-term data on individual social
97 behavior with the extensive pedigree available for the well-studied Amboseli baboon population.
98 Importantly, this dataset allows us to investigate genetic variance in affiliative social behaviors at the
99 level of the individual, as well as indirect genetic effects for affiliative social behavior at the level of the
100 dyadic social relationship. Specifically, we investigate the heritability and genetic architecture (including
101 IGEs) of social grooming, a common affiliative behavior in primates with known links to the survival
102 component of fitness (Silk et al. 2003, Silk et al. 2010, Archie et al. 2014, Campos et al. 2020).

103

104 **Grooming behavior in nonhuman primates**

105 In most non-human primates (the lineage most closely related to humans), grooming interactions
106 represent a very important affiliative behavior (Silk 1987, Dunbar 1991; Silk 2007; Cords 2012) but to
107 date, no work has investigated the quantitative genetic basis of grooming behavior in the wild.
108 Grooming is a primary means by which many non-human primates establish and maintain
109 differentiated, affiliative social bonds (Silk 1987). In many primate systems, including baboons,
110 individuals demonstrate strong grooming preferences and groom certain partners more than others.
111 Strong and enduring grooming relationships – characterized by frequent, repeated grooming
112 interactions over extended periods of time – are common among kin pairs and also occur between
113 unrelated pairs (Silk 1987). Grooming involves manually picking through and cleaning the fur of debris
114 and ectoparasites and is known to reduce disease risk (Tanaka and Takefushi 1993; Sánchez-Villagra et
115 al. 1998; Akinyi et al. 2013). However, grooming is common even when ectoparasites are eliminated
116 (e.g., in captive primates), and the importance of grooming for social affiliation in primates is widely
117 recognized (Dunbar 1991; Silk 2007; Cords 2012). Social grooming can reduce tension and aggression
118 between individuals (e.g., Saunders and Hausfater 1988), and in some wild populations, social grooming
119 can occupy as much as 20% of an animal’s time budget (Dunbar 1991).

120 In many primate species, grooming relationships are generally reciprocal: within dyads, individuals
121 who give more grooming also receive more grooming (e.g., see meta-analysis in Schino and Aureli 2007;
122 also chimpanzees: Gomes et al. 2009; capuchins: Schino et al. 2009; baboons: Silk and Frank 2009; Silk et
123 al. 2010). In baboons, the most enduring social relationships (those that last years rather than months),
124 tend to be highly reciprocal or ‘equitable’ (Silk et al. 2006, 2010). Thus, the grooming an individual
125 receives and the grooming they give to others are strongly phenotypically correlated, even though these
126 phenotypes may have opposing fitness consequences for an individual animal (see Keverne et al. 1989,

127 Wittig et al. 2008, Akinyi et al. 2013, Young et al. 2014 for benefits of receiving grooming and Dunbar
128 and Sharman 1984, Schino 2007 for the small cost of giving grooming). Importantly, females appear to
129 make decisions about who to groom based partly on the grooming behavior of their social partners
130 (Schino 2007; Schino and Aureli 2007). Thus, if grooming behavior is shaped by an individual's genotype,
131 we predict that grooming behavior will also be strongly influenced by indirect genetic effects.

132

133 **Goals of this analysis**

134 Here, we use data on >100,000 grooming interactions between 224 baboons, collected in the well-
135 studied baboon population of the Amboseli region of Kenya, to pursue three goals (Alberts and Altmann
136 2012, Alberts 2019). First, we describe how grooming behavior – specifically the grooming given by adult
137 females to other adult females (hereafter simply 'grooming given') responds to social and non-social
138 environmental effects. Based on previous studies of grooming in primates, we expect that grooming
139 behavior will be influenced by environmental effects acting on the focal individual as well as features of
140 her social group and social partners. Second, we estimate the variance explained by genetic effects on
141 grooming given, both in the context of the whole social group and in the context of pairs of individuals
142 (i.e., dyads). We expect that grooming given will have a partially heritable basis and be influenced by both
143 direct and indirect genetic effects. Third, we measure the relationship between the direct and indirect
144 genetic effects (DGEs and IGEs) on grooming given. Because grooming is often reciprocated, we anticipate
145 that DGEs and IGEs for grooming given will be positively correlated. We explicitly differentiate between
146 DGEs and IGEs for grooming given to better understand how this affiliative behavior might respond to
147 selection.

148 We address all three goals by employing the 'animal model', a mixed effects linear model that
149 estimates both environmental and genetic sources of variance and covariance in phenotypes (see
150 Methods, also Lynch and Walsh 1998; Kruuk 2004). We consider two measures of grooming
151 phenotypes: (i) an *aggregate* measure of grooming given, for each adult female (i.e., a yearly measure of
152 all the grooming that an adult female gave to all other adult females in the social group, regardless of
153 partner identity), and (ii) a *dyadic* measure of grooming given (i.e., grooming given by an adult female to
154 a specific adult female grooming partner, summarized in a yearly index). With our aggregate measure
155 (Figure 1A), we investigated environmental and direct genetic sources of variance. With our dyadic
156 measure (Figure 1B), we investigated environmental, direct, and indirect genetic sources of variance, as
157 well as the genetic covariance between direct and indirect genetic effects.

158

159 **METHODS**

160 **Study population and grooming data collection**

161 The Amboseli baboon population of southern Kenya has been the subject of ongoing research for
162 five decades (Alberts and Altmann 2012; Alberts 2019). The ancestry of baboons in this population is
163 primarily yellow baboon (*Papio cynocephalus*), but all individuals contain low to moderate levels of
164 genetic admixture from a baboon congener, *P. anubis* (Alberts and Altmann 2001; Vilgalys et al. 2022).
165 All animals in the social groups under study (the 'study groups') are individually recognized on sight
166 based on unique morphological and facial features. All demographic and life-history events (births,
167 maturation events, immigrations, deaths, and emigrations) are recorded as part of the near-daily
168 monitoring of the study groups.

169 Our grooming data consisted of counts of grooming events between adult females, with both the
170 giver and receiver of grooming recorded. We considered grooming events between adult females but
171 not grooming involving males for this analysis: female-female grooming interactions occur entirely in
172 social contexts, while female-male grooming interactions occur in both social and sexual contexts, and
173 male-male interactions are very rare altogether. We therefore limited the scope of our analysis to
174 female-female interactions. Grooming was recorded whenever one animal used both hands to pick
175 through the fur of a second animal. We collected grooming counts during systematic monitoring of the
176 population, following a sampling protocol that is designed to avoid potential biases that could result
177 from uneven sampling of study subjects (see Supplementary Methods).

178 Our study subjects were all adult female baboons ($N=224$) present in the study groups between
179 January 1983 and June 2017 for whom we have known pedigree links and enough genetic material to
180 calculate their anubis-yellow ‘admixture score’ (see Tung et al 2008). Individual admixture scores have
181 been linked with several behavioral traits in this population, including male mating success, partner
182 choice, male-female affiliative behavior, male dominance interactions, and male dispersal (Charpentier
183 et al. 2008, Tung et al. 2012, Franz et al. 2015, Fogel et al. 2021). These results suggest that admixture
184 can affect behavior, prompting us to include admixture as a fixed effect in our models. Females were
185 considered adults if they had attained menarche. The resulting dataset represented 115,149 grooming
186 interactions collected during 1,868 female-years of life, with a median of 400.5 interactions per
187 individual.

188 The research in this study was approved by the Institutional Animal Care and Use Committee
189 (IACUC) at Duke University (no. A273-17-12) and adhered to the laws and guidelines of the Kenyan
190 government.

191

192 **Grooming indices**

193 *Aggregate index of grooming given*

194 To determine the heritability of grooming we used the counts of grooming bouts between adult
195 females to calculate an aggregate grooming index. Specifically, for each adult female in each year of her
196 adult life we calculated a yearly index of *aggregate grooming given*. This index reflects the frequency
197 with which she groomed other adult females, relative to the grooming given by all other adult females
198 (of all ages) alive in the same time period, adjusted for observer effort. Observer effort reflects a
199 combination of the number of person-hours we devote to observations of each group and the size of the
200 group, which varies somewhat across years and across social groups (Figure 1A; see also Supplementary
201 Methods, Figure S1A,S1B and Archie et al. 2014). A female with a positive value for this index in a given
202 year exhibited a relatively high frequency of grooming given to other females in the population in that
203 year; a negative value indicates that she exhibited a relatively low frequency of grooming given to other
204 female in that year.

205

206 *Dyadic index of grooming*

207 In order to measure indirect genetic effects on grooming we calculated a yearly *dyadic grooming*
208 *index* for each pair of adult females that were co-resident in a social group for at least 60 days during the
209 calendar year and that had at least one grooming interaction (Figure 1B). For each pair of co-resident
210 females, we measured both a dyadic index of the grooming given from partner A to partner B, as well as

211 an index of grooming given from partner B to partner A. The dyadic index allowed us to investigate
212 direct genetic effects on grooming given, the indirect genetic effects of social partners, and the
213 correlation between these effects. In contrast, the aggregate index only allowed us to investigate direct
214 genetic effects. We also used the dyadic grooming index to investigate environmental and direct genetic
215 effects, which we expected to corroborate the results of our aggregate grooming measure.

216 Positive values of the dyadic index indicate cases in which an adult female gave high frequencies of
217 grooming to a specific partner relative to all other partner pairs in the population for that year, while
218 negative values indicate cases in which an adult female gave relatively low frequencies of grooming to a
219 specific partner (see Supplementary Methods and Figure S1B for details).

220

221 **The ‘animal model’ approach**

222 To partition the phenotypic variance in these measures of social affiliation into additive genetic and
223 other variance components we combined pedigree information and phenotypic values in a mixed effects
224 model, the ‘animal model’ (see Lynch and Walsh 1998, Kruuk 2004). We constructed our pedigree
225 based on long-term demographic records and on genetic parentage assignment carried out using 7-14
226 microsatellite genotypes. The maternities of all our study subjects were known, but only 77% of the
227 paternities were known. Paternity was based on exclusion and further supported through the use of the
228 likelihood-based paternity assignment program CERVUS 2.0. Levels of confidence for all CERVUS
229 analyses were set at 95%. Our paternity assignments were robust across three estimated rates of error,
230 1%, 5% and 10%. These procedures have become standard in the study population (see Buchan et al.
231 2003, Alberts et al. 2006, Van Horn et al. 2007 for methodological details) and have allowed us to
232 produce a pedigree that includes more than 1,500 individuals (Galezo et al. 2022). The subset of this
233 pedigree necessary to describe the relationships between all 224 of our study subjects consists of 347
234 individuals (see Supplementary Methods). This smaller pedigree has 209 father-offspring pairs, 274
235 mother-offspring pairs, and a maximum of 6 generations within a matriline. It includes 225 maternal
236 half-sibling pairs, 320 paternal half-sibling pairs, and 20 full sibling pairs; some paternal siblings and full
237 siblings in our dataset may be undetected. The average relatedness between any two individuals in our
238 trimmed pedigree is 0.014, although this is probably an underestimate, given missing paternal links.

239 The animal model is a form of linear mixed model in which an individual’s additive genetic effect is
240 estimated as a random effect, allowing the estimation of additive genetic variance in pedigreed
241 populations (Kruuk 2004, Wilson 2009). True breeding values are unknown, but they can be estimated
242 based on the expected covariance in additive genetic effects between relatives (see Lynch and Walsh
243 1998, Kruuk 2004). The matrix form of the animal model can be represented by:

$$244 \quad y = \mathbf{X}\beta + \mathbf{Z}u + e$$

245 where y is the vector of phenotypic observations, β is the vector of fixed effects, u is the vector of
246 random effects, \mathbf{X} and \mathbf{Z} are design matrices relating the fixed effects and random effects to each
247 individual and e is the vector of residual errors. We discuss the robustness of this model to the pedigree
248 structure of our population, grooming interactions between kin, and admixture-related variation in
249 genetic ancestry in the Supplementary Methods.

250

251 **Goal 1: Fixed effects: Social and non-social influences on female grooming behavior**

252 In our quantitative genetic animal models, we included fixed effects of other variables known or
 253 predicted to influence grooming behavior (see Table S1 for complete descriptions). These include (i) age,
 254 (ii) ordinal dominance rank, (iii) group size, (iv) sex ratio, (v) presence of mother, adult daughters, and
 255 adult maternal sisters, (vi) total pedigree relatedness to other adult females in the group (aggregate
 256 index) or the focal's relatedness to the dyadic partner (dyadic index), and (vii) individual admixture score
 257 (Table S1). All fixed effects had a variance inflation factor ≤ 2 and the residual plots do not suggest any
 258 relationship between our residuals and the response variable. The specific metrics we used to model
 259 these effects varied slightly according to whether we were analyzing the aggregate or dyadic index of
 260 grooming (Table S1, Table 1).

261 Including these predictors in our models allowed us to determine the association between these
 262 environmental influences and grooming behavior, while accounting for genetic similarities between
 263 individuals in our dataset. Not only are these environmental effects interesting in their own right, they
 264 are important to include in the animal model because if these predictors are non-randomly distributed
 265 over the pedigree, they can potentially bias the estimates of additive genetic variance for a trait if not
 266 taken into account in the genetic model. (Kruuk and Hadfield 2007; Wilson 2008).

267 Our grooming behavior metrics (both the aggregate and the dyadic index) are corrected for observer
 268 effort, which varies both within and across social groups (see Supplementary Methods for details).
 269 Observer effort is correlated with group size, which means that our estimates of the effect of group size
 270 on grooming behavior may be conservatively biased (see Darlington and Smulders 2001 for a discussion
 271 of this type of bias; Campos et al. 2021 and Supplementary Materials for detailed discussions of our use
 272 of observer effort in calculating the relative frequency of social interactions).

273

274 **Goal 2: Direct and indirect genetic effects on female grooming behavior**

275 *Heritability of grooming given using the aggregate grooming index.* We used the 'asremlr' package
 276 in Rv.3.0.1 (Gilmour et al. 2009) to fit a series of linear mixed models with consistent fixed effect
 277 structures and increasingly complex random effect structures. We modeled the aggregate grooming
 278 behavior of individual i in the following series of nested models:

279

$$\begin{aligned}
 y_{ij} &= \text{fixed effects} + e_{ij} && \text{(null model)} \\
 y_{ij} &= \text{fixed effects} + F_i + e_{ij} && \text{(repeatability model)} \\
 y_{ij} &= \text{fixed effects} + F_i + \text{mom}_i + e_{ij} && \text{(maternal effects model)} \\
 y_{ij} &= \text{fixed effects} + a_{F_i} + pe_{F_i} + \text{mom}_{F_i} + e_{ij} && \text{(heritability model)}
 \end{aligned}$$

280

281 where y_{ij} is the aggregate grooming given by individual i in year j , e_{ij} is a residual error term, F_i is a
 282 random effect of the identity of the focal individual, mom_i is a random effect of the mother of the focal
 283 individual, a_{F_i} is the additive genetic contribution of individual i (i.e., its breeding value) and
 284 pe_{F_i} represents the 'permanent environmental' effect of individual i . Permanent environmental effects
 285 represent sources of variance between individuals that arise through environmental effects. We did not
 286 include a random effect of year because the aggregate index was standardized across years (see
 287 Supplementary Methods). We used a likelihood ratio test to determine the best fit model for each
 288 grooming index. Including the fixed effects described in Goal 1 could reduce the residual variance

289 reported in our models which may alter our heritability estimates. Therefore, following common
 290 practice, we report heritability estimates from models with and without fixed effects (see Results).

291
 292 *Direct and indirect genetic effects on grooming given, using the dyadic grooming index.* We next
 293 fitted a series of linear mixed models using the dyadic grooming index, again using the ‘asremlr’ package
 294 (Gilmour et al. 2009). The primary benefit of the dyadic grooming index is that it allowed us to
 295 investigate indirect genetic effects on grooming, something that is not possible with the aggregate
 296 indices.

297 To determine whether indirect genetic variance contributes significantly to phenotypic variance in
 298 the dyadic grooming index, we constructed five nested models, with consistent fixed effects (as
 299 described above for the aggregate measures) and increasingly complex random effect structures. We
 300 followed the approach outlined by Wilson et al. (2011) in their investigation of indirect genetic effects
 301 for aggressive phenotypes. Specifically, we modeled the grooming given from a focal individual i to a
 302 grooming partner j in a series of five models:

303

$$y_{ijk} = \text{fixed effects} + dyad_{ij} + e_{ijk} \quad (\text{null model})$$

$$y_{ijk} = \text{fixed effects} + F_i + dyad_{ij} + e_{ijk} \quad (\text{repeatability model})$$

$$y_{ijk} = \text{fixed effects} + F_i + P_j + dyad_{ij} + e_{ijk} \quad (\text{repeatability with partner model})$$

$$y_{ijk} = \text{fixed effects} + a_{F_i} + pe_{F_i} + P_j + dyad_{ij} + e_{ijk} \quad (\text{direct genetic effects model})$$

$$y_{ijk} = \text{fixed effects} + a_{F_i} + pe_{F_i} + a_{P_j} + pe_{P_j} + dyad_{ij} + e_{ijk} \quad (\text{indirect genetic effects model})$$

304 where y_{ijk} is the grooming given from individual i to individual j in year, k and $dyad_{ij}$ is an identity
 305 assigned to each unique pair of individuals. This term is included because we have repeated measures
 306 across each dyad in the dataset. The fixed effects, F_i , a_{F_i} , pe_{F_i} and e_{ijk} terms are as described above
 307 under Goal 2. P_j is a random effect of the partner individual who received grooming, a_{P_j} is the additive
 308 genetic contribution of the individual who received grooming and pe_{P_j} is the permanent environment
 309 effect of the individual who received grooming. The ‘direct genetic effects’ model allows genetic
 310 variance among the focal individuals to influence phenotypic variance in grooming given, while the
 311 ‘indirect genetic effects model’ allows genetic variance among both the focal and the partner individuals
 312 to influence phenotypic variance in grooming given by the focal partner. In the indirect genetic effects
 313 model, direct and indirect genetic effects were free to covary, and we estimated the covariance
 314 between the direct genetic effects on grooming given (a_F) and the indirect genetic effects on grooming
 315 given (a_P).

316
 317 As with Goal 1, because these models are nested with respect to their random effects, we used a
 318 likelihood ratio test to determine the best model for the dyadic grooming index. We also tested models
 319 that included random effects of social group and the focal individual’s mother and found no statistically
 320 significant variation explained by these effects.

321
 322 **Goal 3: Covariance between DGEs and IGEs, using the dyadic grooming index.**

323 To investigate the covariance between direct and indirect genetic effects on our dyadic index of
324 grooming given, we began with the indirect genetic effects model described above, in which we allowed
325 a relationship between two random effects (focal breeding value and partner breeding value) so that
326 the model fit an unstructured 2x2 matrix, which supplied the genetic variances for the giver and receiver
327 in the diagonal, and the covariance on the off-diagonal (see *Example Code* in Supplement and McFarlane
328 et al. 2015 for more details about this approach). We rescaled the covariance to a correlation and to
329 determine if this correlation was significantly different from 0 and/or significantly different from +1, we
330 used a likelihood ratio test with one degree of freedom to compare the model in which the correlation
331 between IGEs and DGEs was free to vary with models in which this correlation was constrained to either
332 0 or 1.

333 We also calculated the ‘total heritability’ of our dyadic index of grooming given, following Bijma et
334 al. (2007) and Wilson et al. (2009) as $\sigma_{A_F}^2 + 2\sigma_{A_F, A_P} + \sigma_{A_P}^2$ divided by the total phenotypic variation. The
335 total heritability metric describes the proportion of the variance in grooming given in the dyadic index
336 that is explained by genetic variation in both focal and partner individuals. This metric also takes into
337 account the correlation between IGEs and DGEs, potentially making it a more useful predictor of how a
338 trait shaped by interactions between individuals may respond to selection.

339

340 RESULTS

341 Goal 1: Fixed effects: Social and non-social influences on female grooming behavior

342 Younger females and higher-ranking females tended to give more aggregate grooming, as did
343 females who spent more time co-resident with their mothers and adult daughters. The amount of
344 aggregate grooming given was not influenced by time spent co-resident with maternal sisters, total
345 relatedness to other females in the group, or focal admixture score (Table 1, S2). Group size did not
346 influence the amount of aggregate grooming given, but we note that our analysis may underestimate
347 the strength of this effect because we corrected our measure of grooming for observer effort, which is
348 correlated with group size (see Supplement for details).

349 The environmental predictors of dyadic grooming given were similar to those for aggregate
350 grooming given (Table 1, S2). The dominance ranks of the focal female and her partner interacted, such
351 that high-ranking females gave more grooming to high-ranking females than to low-ranking females, and
352 low-ranking females gave more grooming to low-ranking females than to high-ranking females (Table 1,
353 Figure S2). Individuals gave more grooming when their partners were relatives than when their partners
354 were non-relatives, and gave more grooming when their partners were their mothers, daughters, or
355 maternal sisters than to other types of partners, even when controlling for relatedness. We also
356 detected a statistically significant effect of group size on the dyadic index, such that females gave less
357 grooming to each female grooming partner when they were in larger group; we again note that our
358 analysis may underestimate the strength of this effect (see Supplement for details). As with the
359 aggregate index, we found no effect of admixture score on dyadic grooming (Table 1, S2).

360

361 Goal 2: Direct and indirect genetic effects on female grooming behavior

362 *Heritability of aggregate grooming given.* The heritability model was the best model for our
363 aggregate index of grooming given, with a heritability estimate of $h^2=0.22 \pm 0.048$ (Table 2, Figure S3).

364 This heritability estimate represents the proportion of variance explained by additive genetic variance
365 after conditioning on the fixed effects we included in our model. Conditioning on fixed effects has the
366 potential to significantly affect heritability estimates (see Methods and Wilson 2008). Therefore, we also
367 ran parallel models that excluded fixed effects, which generated very similar heritability estimates
368 ($h^2=0.30 \pm 0.07$, Table S3).

369
370 *Direct and indirect genetic effects on grooming given, using the dyadic index.* The IGE model was the
371 best model among those we tested for the dyadic grooming index (Table 3, Figure S4). Because this
372 model allowed additive genetic variance within focal *and* partner individuals to contribute to variance in
373 grooming given, this result indicates measurable indirect genetic effects of partner identity on the
374 amount of grooming that a focal female gave within a dyadic partnership. However, estimates of both
375 direct and indirect genetic effects on the dyadic index were small: indirect genetic effects (i.e., genetic
376 variation among partner individuals in the IGE model in Table 3) explained approximately 2% of the
377 variance in how much grooming a female gave to a particular female partner, and direct genetic effects
378 (in the DGE model in Table 3) explained 4.8%. The large difference in the magnitude of direct genetic
379 effects between the dyadic model and the aggregate model (where direct genetic effects explain 22% of
380 variance in the aggregate index) likely arises from the fact that any given dyad in the IGE dataset has
381 many fewer interactions than any given focal individual in the aggregate index used in the DGE-only
382 model. As a result, small errors in measurement have a larger effect on our dyadic index than our
383 aggregate index; these errors in measurement likely inflate the residual (error) variance in our dyadic
384 index and produce a conservative estimate of both direct and indirect genetic effects.

385 **Goal 3: Covariance between DGEs and IGEs**

387 Indirect and direct genetic effects (IGEs and DGEs) for grooming given were strongly positively
388 correlated ($r=0.74 \pm 0.09$, $p<0.0001$). To determine if this correlation was significantly different from
389 both 0 and 1, we compare the model in which the correlation between IGEs and DGEs was free to vary
390 (shown in Table 3, last row) with models in which this correlation was constrained to either 0 or 1, using
391 a likelihood ratio test. The model that allowed the genetic correlation to freely vary was the best model
392 and was significantly different from the other two: $p<0.0001$ for the comparison with the model in
393 which the covariance was constrained to 0, and $p=0.006$ for the comparison with the model in which the
394 covariance was constrained to 1). This positive correlation between IGEs and DGEs suggests that
395 specific genetic variants predict increased grooming given by focal individuals, whether those variants
396 are found in the focals themselves or in their grooming partners.

397 The total heritability of our dyadic index of grooming given was $h^2=0.127 (\pm 0.023)$. This heritability
398 metric represents the proportion of variance in the trait explained by genetic effects after conditioning
399 on the fixed effects included in the dyadic model. Notably, the total heritability estimate, which takes
400 into account indirect genetic effects and the correlation between direct and indirect genetic effects, is
401 more than twice the heritability estimate based on direct genetic effects alone in our IGE model.

402 **DISCUSSION**

404 Here, we provide one of the first empirical estimates of indirect genetic effects on affiliative social
405 behavior in the wild. Our analysis reveals that a focal female's genotype influences the extent to which

406 she grooms her social partners, and her partners' genotypes also appear to influence the focal female's
407 grooming behavior, although this effect is smaller. Furthermore, the genotypes that encourage a female
408 to give grooming *to* her social partners also may be genotypes that elicit grooming *from* her social
409 partners. We discuss our main findings below.

410

411 **Goal 1: Fixed effects: Social and non-social sources of variance in grooming behavior**

412 The environmental and demographic factors that influence female grooming behavior have been
413 investigated in a number of primate species, including baboons (Schino 2001; Nakamichi 2003; Lehmann
414 et al. 2007; Akinyi et al. 2013). Our analysis is unique because, by incorporating pedigree information in
415 the animal model, our estimates of fixed environmental effects account for pseudo-replication that may
416 occur by including individuals with similar genetic backgrounds. Three types of environmental effects on
417 grooming are particularly noteworthy.

418 *Dominance rank.* Our results are consistent with the observation, widely documented across
419 primate species, that higher-ranking females have more grooming partners than lower-ranking females.
420 This pattern is consistent with the well-supported hypothesis, first proposed by Seyfarth (1977), that
421 females groom higher ranking individuals in exchange for currencies other than grooming (e.g., agonistic
422 support, tolerance during feeding, etc.; see Seyfarth 1977; Schino 2001). In addition, while we found no
423 main effect of dominance rank on dyadic grooming, we did find an interaction effect, such that higher-
424 ranking individuals gave more grooming to high-ranking partners, while lower-ranking individuals gave
425 more grooming to low-ranking partners (Table 1). This result parallels a previous analysis of male-female
426 grooming in this population, in which the probability of grooming was highest for male-female pairs in
427 which both partners were high-ranking (Fogel et al 2021). This result is also consistent with Seyfarth's
428 model, which predicts that females compete for the opportunity to groom higher ranking females, and
429 consequently high-ranking females have the greatest access to their preferred partners (Seyfarth 1977).

430 *Demographic effects.* Group size did not have a significant effect on aggregate grooming given, but
431 females gave less grooming to individual partners in larger groups. Females engaged in more grooming
432 in groups with a more female biased sex ratio. In combination, these results suggest that females in
433 larger groups have more female grooming partners than females in smaller groups but groom each
434 partner less when they are in a larger group, pointing towards a potential tradeoff between the strength
435 and quantity of social bonds with females. This result is consistent with other studies that have found
436 evidence of a decrease in group cohesion with increasing group size (Dunbar 1991; Henzi et al. 1997;
437 Lehmann et al. 2007; Cheney et al. 2012).

438

439 **Goal 2: Direct and indirect genetic effects on female grooming behavior**

440 We found that the tendency to engage in affiliative social interactions with other females is
441 heritable and consequently, may evolve in response to natural selection. The heritability we detected
442 for aggregate grooming given was 0.22, consistent with heritability estimates reported for life history
443 and behavioral traits in wild populations, but lower than generally reported for morphological traits
444 (Visscher et al. 2008, Houslay et al. 2021). This result provides an important conceptual link between
445 studies that have demonstrated apparent fitness benefits of social interactions, and studies that have
446 demonstrated heritability for phenotypes that influence social interactions (e.g., physiology: Insel and
447 Shapiro 1992; Walum et al. 2008; Staes et al. 2018; personality: Jang et al. 1996; Brent et al. 2014; Staes

448 et al. 2016; morphology: Moore 1990; Schielzeth et al. 2012). However, further work is needed to
449 predict the magnitude and direction of any response to selection. While we have strong evidence
450 linking grooming behavior to both health (Akinyi et al. 2013) and survival in this study population (Silk et
451 al. 2003; Archie et al. 2014; Campos et al. 2020), we do not yet know whether grooming behavior has a
452 causal link to survival or is simply correlated with other traits that do.

453 Our estimates of indirect genetic effects were small but measurable, accounting for 2% of the
454 variance in how much grooming a female gave to a particular female partner. As noted in the Results
455 section, any given dyad in the IGE dataset has many fewer interactions than any given focal individual in
456 the DGE-only model. Therefore, small errors in measurement have a larger effect on our dyadic index
457 than our aggregate index, contributing to large residual (error) variance in our dyadic index and limiting
458 our ability to detect IGEs. Thus, we view our estimate of IGEs for grooming as conservative.

459

460 **Goal 3: The genetic relationship between grooming given and grooming received**

461 The total heritability we detected for dyadic grooming given was 0.127. This metric reflects the
462 proportion of variance in dyadic grooming that is explained by genetic effects of both the focal and the
463 partner individual –i.e., direct genetic effects (genetic variation in focal individuals), and indirect genetic
464 effects (genetic variation in partner individuals). It also provides insight into how the relationship
465 between DGEs and IGEs may alter the evolutionary potential of the trait. Although our estimates of IGEs
466 alone were small (0.02 ± 0.005), including them in our model doubled our estimate of the total
467 heritability of dyadic grooming given compared to a dyadic model that included DGEs alone, because of
468 the positive correlation between IGEs and DGEs for dyadic grooming given. This result is consistent with
469 the expectation that IGEs are an important part of the genetic architecture of grooming given and
470 suggests that grooming behavior may respond to selection more strongly than we would expect from
471 considering DGEs alone. Our results are the first demonstration, to our knowledge, of indirect genetic
472 effects on affiliative social behaviors in a wild vertebrate population. IGEs are thought to be of particular
473 importance in the evolution of social behavior compared to other phenotypes (Wolf et al. 1998; Moore
474 et al. 2002; Cheverud 2003; McGlothlin et al. 2010, Bailey et. al 2018), and our study stands as an
475 important example of the feasibility of measuring IGEs for social behavior in the wild.

476 What explains the strong correlation between the direct and indirect genetic effects on grooming
477 given ($R=0.74 \pm 0.09$)? A possible explanation for the strong correlation between IGEs and DGEs for
478 grooming given is that the tendency for an individual to give grooming and the tendency for an
479 individual to elicit grooming from their social partners emerge from the same underlying, partially
480 heritable trait. One candidate trait would be the tendency to reciprocate when groomed. As noted
481 earlier, individuals tend to form highly reciprocal grooming relationships in many primate species (Schino
482 and Aureli 2007), and in baboons the most enduring social relationships are the most reciprocal ones
483 (Silk et al. 2006a, 2010). It is possible that our grooming data do not simply reflect the tendency to give
484 and elicit grooming *per se*, but instead reflect primarily the tendency to reciprocate when groomed. That
485 is, given that individual A begins a grooming relationship with individual B at some point in its life, it is
486 possible that much of the grooming we subsequently measure between A and B depends on each
487 partner's tendency to reciprocate grooming. If individuals assort socially according to their tendency to
488 reciprocate (so that high reciprocators tend to prefer each other), the result would be a strong positive

489 correlation between grooming and being groomed, which emerges from the genetic identity of these
490 traits or a strong genetic correlation between them.

491 An additional strategy for investigating whether the genetic correlation between grooming given
492 and grooming received can be explained by reciprocity would involve trait-based investigations of
493 indirect genetic effects (see Wolf et al. 1998; Bleakley and Brodie IV 2009; McGlothlin and Brodie 2009).
494 Trait-based approaches focus on how phenotypes are influenced by specific traits in a social partner, as
495 opposed to simply estimating the proportion of variance in the focal phenotype explained by similarity
496 in the partner's genotype, as we did here (see also Wilson et al. 2005, 2009, 2011; Sartori and
497 Mantovani 2012). Our approach, a 'variance-partitioning method,' is useful for initial estimates of direct
498 and indirect genetic effects and genetic covariance and is well suited to the genetic structure of our
499 natural breeding population. Future analyses using a trait-based approach would generate further
500 insight into the mechanistic basis of the observed reciprocity. However, a trait-based approach would
501 require fine-grained phenotypic data on the duration and sequential order of grooming bouts, which is
502 not a part of our standard behavioral data collection protocol.

503 It will be challenging to determine whether the correlation between direct and indirect effects on
504 grooming given does indeed reflect genetic identity between these two apparently distinct traits, or the
505 effects of pleiotropic alleles acting on grooming given and grooming elicited, or something else: animal
506 models are not designed to identify causal relationships and consequently we interpret our results with
507 caution. Whatever the underlying explanation, our results indicate an important role for genetic
508 architecture in the evolution of cooperation and reciprocity in primates. An illustrative example has
509 been documented in microbes such as the social amoeba *Dictyostelium discoideum* (see also, Rainey and
510 Rainey 2003; Griffin et al. 2004; Xavier and Foster 2007; Springer et al. 2011). Under certain conditions,
511 some *D. discoideum* cells die to form a stalk that facilitates the dispersal of other cells in reproductive
512 spores (Strassmann et al. 2000). This pattern of stalk formation is often interpreted as an act of extreme
513 cooperation and even altruistic sacrifice. Genetic architecture, namely pleiotropy, has been implicated
514 in preventing cheaters who avoid the sacrifice of stalk formation from achieving the reproductive
515 benefits of spore production. Foster et. al (2004) showed that the *dimA* gene is required for both
516 differentiation into the cooperative stalk, and for correct allocation to the reproductive spore. The
517 pleiotropic effects of this gene mean that cheating genotypes that avoid the sacrifice of the cooperative
518 stalk also fail to allocate correctly to the reproductive spore. This genetic architecture serves to
519 facilitate the evolution of cooperation by preventing the spread of cheaters.

520 The correlation between the IGEs and DGEs for grooming that we report here suggests the
521 possibility that mechanisms similar to those described for *Dictyostelium discoideum* could potentially be
522 at work in multicellular social organisms. Specifically, strong genetic linkages between reciprocity-
523 related phenotypes may make it difficult for cheaters (e.g., those who do not give grooming in response
524 to receiving it) to emerge and invade. In this scenario, a strong genetic correlation between the
525 tendency to provide grooming and the tendency to elicit grooming from social partners would have an
526 effect similar, in principle, to the pleiotropic *dimA* effect in *D. discoideum*.

527

528 **Future directions**

529 The work described here integrates primate behavioral ecology and quantitative genetics. We hope
530 this integration serves to advance both fields, as behavioral ecology investigates how behavior might

531 evolve in response to ecological and environmental pressures, and quantitative genetics provides the
532 information needed to build realistic evolutionary models that consider the genetic (co)variation in traits
533 (Cheverud and Moore 1994).

534 Many previous studies have investigated variation in primate grooming behavior, providing a strong
535 framework for interpreting our results (e.g., Silk 1987; Keverne et al. 1989; Dunbar 1991; Sánchez-
536 Villagra et al. 1998; Silk 2007; Schino and Aureli 2007; Gomes et al. 2009; Schino et al. 2009; Wittig et al.
537 2008, Cords 2012; Akinyi et al. 2013). Our study is the first to carry out such an investigation while
538 simultaneously controlling for genetic relatedness between individuals. Our results were broadly
539 consistent with previous studies, with some surprising exceptions that may be due to methodological
540 constraints. For instance, we found that group size affected dyadic grooming, but not aggregate
541 grooming given. This may imply that females adjust their number of grooming partners in response to
542 group size, but do not adjust the total time spent grooming. Alternatively, aggregate grooming given
543 may be affected by group size in our population and our ability to detect that effect in this study may be
544 reduced by our methodological correction for observer effort. We were also surprised that age and
545 admixture score had no effect on dyadic grooming in our study, as previous work in our population has
546 indicated that younger animals receive more grooming than older animals (Akinyi et al. 2013) and that
547 individuals with higher admixture scores preferential groom each other (Fogel et al. 2021). However, we
548 note that variance in dyadic grooming explained by either of these parameters may be fully captured by
549 the “dyad” term in our model as the relative ages and admixture scores of partners in a dyad were likely
550 unique to each specific dyad in our study. Our study was designed to investigate the role of genetic
551 variance in grooming behavior; future studies designed to more closely investigate the role of group
552 size, age and genetic admixture on grooming may shed light on these results.

553 This work is a relatively rare example of an analysis of both genetic variance and indirect genetic
554 effects in affiliative social behavior in a wild vertebrate. The measurable heritability that we report for
555 grooming behavior—a trait previously linked to survival—motivates a more detailed analysis of the
556 magnitude of the phenotypic response to selection on grooming behavior. Furthermore, the IGE-DGE
557 covariance that we document is intriguing in light of the theoretical potential for IGEs and for IGE-DGE
558 covariance to fundamentally shape the evolution of social traits (e.g., Wilson et al. 2009, Bijma and
559 Wade 2008, McGlothlin al 2010). Few empirical studies have estimated the complete set of necessary
560 parameters to predict how social traits respond to selection, including DGEs, IGEs, their covariance,
561 relatedness within the group, group size and measures of direct and social (or individual and group level)
562 selection gradients (Bijma and Wade 2008). We have laid the groundwork for such an investigation here
563 by estimating the relevant quantitative genetic parameters. Estimates of relevant selection gradients
564 are still needed for understanding short-term evolutionary dynamics of grooming, but these will become
565 increasingly feasible to generate as data collection at this long-term field study continues.

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