

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

Emily M. McLean^{1,2}, Jacob A. Moorad³, Jenny Tung^{4,5,6,7}, Elizabeth A. Archie⁸, Susan C. Alberts^{4,5,6}

¹University Program in Genetics and Genomics, Duke University, Durham, NC, United States

²Division of Natural Sciences and Mathematics, Oxford College, Emory University, Oxford, GA, United States

³Institute of Ecology and Evolution, University of Edinburgh, Edinburgh, Scotland

⁴Department of Biology, Duke University, Durham, NC, United States

⁵Department of Evolutionary Anthropology, Duke University, Durham, NC, United States

⁶Population Research Institute, Duke University, Durham, NC, United States

⁷Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁸Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, United States

Corresponding author: Division of Natural Sciences and Mathematics, Oxford College, Emory University, Oxford, GA, United States. Email: emily.mclean@emory.edu

Abstract

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

Keywords: indirect genetic effects, social behavior, grooming, heritability, primate behavior

Introduction

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

Given the links between affiliative social interactions and fitness-related traits in highly social species, natural selection probably favors individuals who are more affiliative with conspecifics. However, despite the clear and compelling links between affiliative social behavior and fitness-related traits, we have a limited understanding of how affiliative social

behavior evolves. Addressing this question requires understanding the genetic architecture of highly social traits, as well as determining the relative contributions of genetic and environmental variation to phenotypic variation in wild populations where natural selection is acting. Specifically, for an evolutionary response to selection to occur, phenotypic variation in affiliative social behavior must have an underlying heritable component.

Furthermore, when a trait is affected by interactions between individuals, its genetic architecture is determined not only by the focal individual's own genotype (i.e., direct genetic effects, or DGEs) but by the genotype of its partner(s) (i.e., indirect genetic effects, or IGEs; (reviewed in Baud et al., 2022; McGlothlin et al., 2010; Moore et al., 1997)). Some of the most well-documented examples of IGEs occur between mothers and offspring (e.g., maternal genetic effects), which occur when the offspring's phenotype is influenced by the genotype of its mother, independently of the direct effects of the genes the offspring inherits. For example, maternal genotype explains 11% of the variance in offspring birth weight in a feral population of Soay sheep (Wilson et al., 2005) and 31% of the variance in birth weight in red deer (Gauzere et

al., 2020). Indirect genetic effects between unrelated partners can also be substantial: in a study of Eastern chipmunks, 23% of the variance in fecundity and 36% of the variance in “trapability” (the number of times captured) were explained by IGEs (Santostefano et al., 2021).

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

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

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

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

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

Grooming behavior in nonhuman primates

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

In many primate species, grooming relationships are generally reciprocal: within dyads, individuals who give more grooming also receive more grooming (e.g., see meta-analysis in Schino & Aureli, 2007; also chimpanzees: Gomes et al., 2009; capuchins: Schino et al., 2009; baboons: Silk & Frank, 2009; Silk et al., 2010). In baboons, the most enduring social relationships (those that last years rather than months), tend to be highly reciprocal or “equitable” (Silk et al., 2006, 2010).

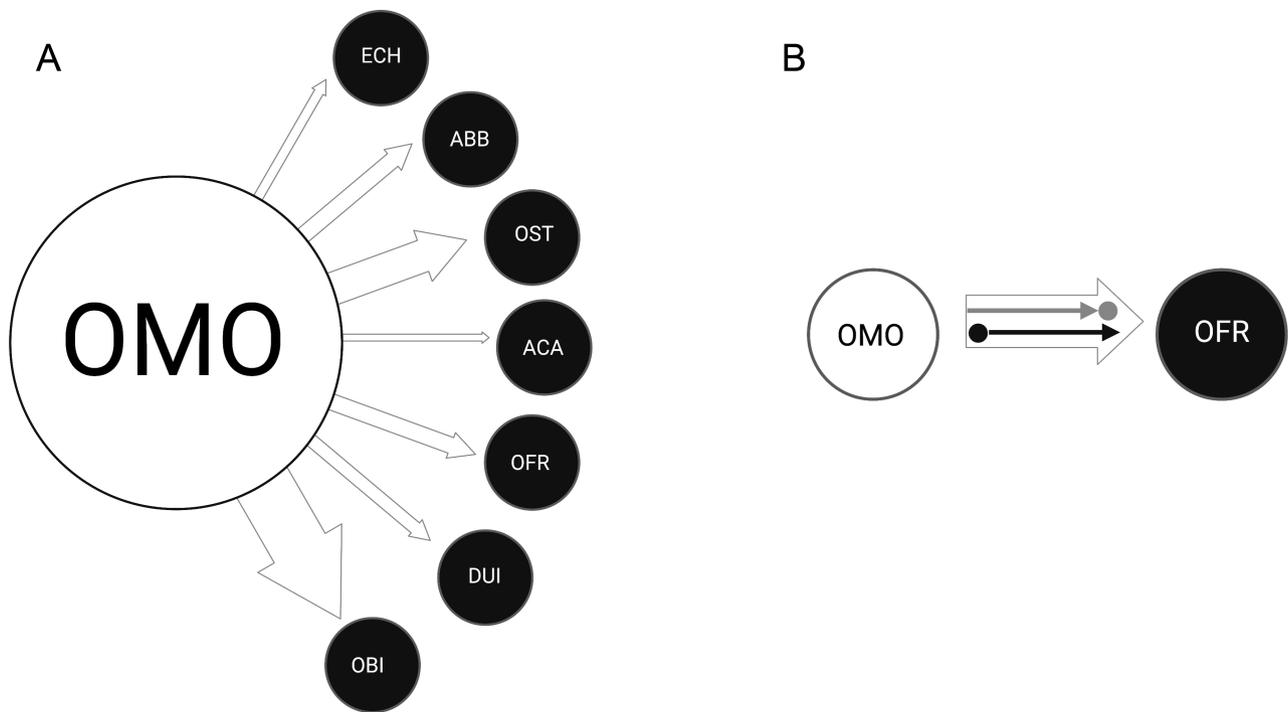


Figure 1. Visualization of grooming metrics. (A) An example of our aggregate grooming index, representing grooming given by an adult female baboon OMO in 2003, considering all other adult females in her social group that year (individual females are identified by three-letter codes). Block arrows represent grooming given by OMO. The width of the arrow indicates the relative frequency of grooming observed; wider arrows indicate higher relative frequencies. OMO’s aggregate grooming given for 2003 is the sum of the width of the block arrows. (B) An example of our dyadic index. Here, we observed the grooming given by OMO to adult female OFR in a single year, represented by the large, gray block arrow. This phenotype is shaped by two components: the tendency of OMO to give grooming (direct effects), represented by the small gray arrow pushing the gray ball, and the tendency of OFR to elicit grooming from her partners (indirect effects) represented by the small black arrow pulling the black ball.

Thus, the grooming an individual receives and the grooming they give to others are strongly phenotypically correlated, even though these phenotypes may have opposing fitness consequences for an individual animal (see Akinyi et al., 2013; Keverne et al., 1989; Wittig et al., 2008; Young et al., 2014 for benefits of receiving grooming and Dunbar & Sharman, 1984; Schino, 2007 for the small cost of giving grooming). Importantly, females appear to make decisions about who to groom based partly on the grooming behavior of their social partners (Schino, 2007; Schino & Aureli, 2007). Thus, if grooming behavior is shaped by an individual’s genotype, we predict that grooming behavior will also be strongly influenced by indirect genetic effects.

Goals of this analysis

Here, we use data on >100,000 grooming interactions between 224 baboons, collected in the well-studied baboon population of the Amboseli region of Kenya, to pursue three goals (Alberts, 2019; Alberts & Altmann, 2012). First, we describe how grooming behavior—specifically the grooming given by adult females to other adult females (hereafter simply “grooming given”) responds to social and non-social environmental effects. Based on previous studies of grooming in primates, we expect that grooming behavior will be influenced by environmental effects acting on the focal individual as well as features of her social group and social partners. Second, we estimate the variance explained by genetic effects on grooming given, both in the context of the whole social group and in the context of pairs of individuals (i.e., dyads). We expect that grooming given will

have a partially heritable basis and be influenced by both direct and indirect genetic effects. Third, we measure the relationship between the direct and indirect genetic effects (DGEs and IGEs) on grooming given. Because grooming is often reciprocated, we anticipate that DGEs and IGEs for grooming given will be positively correlated. We explicitly differentiate between DGEs and IGEs for grooming given to better understand how this affiliative behavior might respond to selection.

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

Methods

Study population and grooming data collection

The Amboseli baboon population of southern Kenya has been the subject of ongoing research for five decades (Alberts,

2019; Alberts & Altmann, 2012). The ancestry of baboons in this population is primarily yellow baboon (*Papio cynocephalus*), but all individuals contain low to moderate levels of genetic admixture from a baboon congener, *P. anubis* (Alberts & Altmann, 2001; Vilgalys et al., 2022). All animals in the social groups under study (the “study groups”) are individually recognized on sight based on unique morphological and facial features. All demographic and life-history events (births, maturation events, immigrations, deaths, and emigrations) are recorded as part of the near-daily monitoring of the study groups.

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

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

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

Grooming indices

Aggregate index of grooming given

To determine the heritability of grooming, we used the counts of grooming bouts between adult females to calculate an aggregate grooming index. Specifically, for each adult female in each year of her adult life, we calculated a yearly index of *aggregate grooming given*. This index reflects the frequency with which she groomed other adult females, relative to the grooming given by all other adult females (of all ages) alive in the same time period, adjusted for observer effort. Observer effort reflects a combination of the number of person-hours we devote to observations of each group and the size of the group, which varies somewhat across years and across social groups ([Figure 1A](#); see also [Supplementary Methods](#), [Supplementary Figure S1A, B](#) and [Archie et al., 2014](#)). A

female with a positive value for this index in a given year exhibited a relatively high frequency of grooming given to other females in the population in that year; a negative value indicates that she exhibited a relatively low frequency of grooming given to other females in that year.

Dyadic index of grooming

In order to measure indirect genetic effects on grooming we calculated a yearly *dyadic grooming index* for each pair of adult females that were co-residents in a social group for at least 60 days during the calendar year and that had at least one grooming interaction ([Figure 1B](#)). For each pair of co-resident females, we measured both a dyadic index of the grooming given from partner A to partner B, as well as an index of grooming given from partner B to partner A. The dyadic index allowed us to investigate direct genetic effects on grooming given, the indirect genetic effects of social partners, and the correlation between these effects. In contrast, the aggregate index only allowed us to investigate direct genetic effects. We also used the dyadic grooming index to investigate environmental and direct genetic effects, which we expected to corroborate the results of our aggregate grooming measure.

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

The “animal model” approach

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

Table 1. Social and non-social environmental effects on aggregate and dyadic grooming indices.

	Aggregate grooming given	Dyadic grooming index	Interpretation of effect size directions and estimates
Individual traits			
Focal dominance rank	$\beta = -0.01 (\pm 0.006)^{\dagger}$ $p = .049$	$\beta = -0.033 (\pm 0.006)$ $p = .06$	Aggregate index: higher ranking females (those with lower numerical rank, e.g., 1, 2, 3) gave more grooming than lower ranking females. The estimate represents the expected change in the grooming index in response to an increase of one numerical focal rank position. Dyadic index: no effect.
Partner dominance rank	NA ^{††}	$\beta = -0.026 (\pm 0.004)$ $p = .92$	Dyadic index: no effect.
Focal-partner rank interaction	NA	$\beta = 0.002 (\pm 0.0003)$ $p < .0001$	Dyadic index: High ranking focals groomed high ranking partners more than they groomed low ranking partners. Low ranking focals groomed low ranking partners more than they groomed high ranking partners (Supplementary Figure S3).
Focal age	$\beta = -0.09 (\pm 0.006)$ $p < .0001$	$\beta = -0.025 (\pm 0.006)$ $p < .0001$	Aggregate index: Younger females gave more grooming. The estimate represents the expected change in the grooming index in response to a one year increase in age. Dyadic index: Focal females gave less grooming to their partners when they (the focals) were older. The estimates represent the expected change in each grooming index in response to a one year increase in focal age.
Partner age	NA	$\beta = 0.011 (\pm 0.006)$ $p = .07$	Dyadic index: no effect
Focal-partner age interaction	NA	$\beta = -0.0007 (\pm 0.0006)$ $p = .15$	Dyadic index: no effect.
Family effects			
Co-residency with mother	$\beta = 0.14 (\pm 0.059)$ $p = .017$	NA	Aggregate index: Females who spent more of the time period co-residing with their mother gave more grooming. The estimate represents the expected difference in aggregate grooming given between females that spent none of the time period with their mom and females that spent 100% of the time period with their mom.
Co-residency with adult daughters	$\beta = 0.37 (\pm 0.035)$ $p < .0001$	NA	Aggregate index: Females who spent more of the time period co-residing with adult daughters gave more grooming. The estimate represents the expected difference in aggregate grooming given between females that spent none of the time period with any adult daughters and females that spent 100% of the time period with an average of 1 adult daughter.
Co-residency with adult maternal sisters	$\beta = -0.02 (\pm 0.027)$ $p = .457$	NA	Aggregate index: no effect
Pedigree relatedness to other adult females	$\beta = 0.03 (\pm 0.063)$ $p = .60$	NA	Aggregate index: no effect.
Mother-daughter pair	NA	$\beta = 1.67 (\pm 0.095)$ $p < .0001$	Dyadic index: Focal females groomed more when their partner was their mother than when the partner was not their mother. The estimate represents the expected difference in the dyadic grooming index for mother-daughter pairs compared to pairs who were not mother-daughter.
Maternal sister pair	NA	$\beta = 0.58 (\pm 0.064)$ $p < .0001$	Dyadic index: Focal females groomed more when their partner was their maternal sister than when their partners was not a maternal sister. The estimate represents the expected difference in the dyadic grooming index for maternal sister pairs compared to pairs who were not maternal sisters
Relatedness to partner	NA	$\beta = 0.68 (\pm 0.182)$ $p = 0.002$	Dyadic index: Focal females groomed more when their partner was more closely related to them, and less when their partner was less closely related to them. The estimate represents the expected change in the dyadic grooming index as partner relatedness changed from 0 to 1.

Table 1. Continued

	Aggregate grooming given	Dyadic grooming index	Interpretation of effect size directions and estimates
Demographic effects			
Group size	$\beta = -0.01 (\pm 0.003)$ $p = 0.124$	$\beta = -0.01 (\pm 0.002)$ $p < .0001$	Aggregate index: No effect. Dyadic index: Focal females gave less grooming to each social partner in larger groups. The estimates represent the expected change in each grooming index in response to an increase in group size of one group member.
Sex ratio	$\beta = 0.05 (\pm 0.027)$ $p = .646$	$\beta = 0.02 (\pm 0.016)$ $p = .25$	Aggregate and dyadic indices: No effect.
Admixture effects			
Focal admixture score	$\beta = 0.36 (\pm 0.200)$ $p = .07$	$\beta = 0.24 (\pm 0.125)$ $p = .11$	Aggregate and dyadic indices: No effect.
Partner admixture score	NA	$\beta = 0.11 (\pm 0.099)$ $p = .58$	Dyadic index: No effect.
Focal-partner admixture score interaction	NA	$\beta = -0.291 (0.207)$ $p = .29$	Dyadic index: No effect.

Bold text indicates effects with $p < .05$.

[†] The top line of each row provides the effect size estimate and standard error for each fixed effect.

^{††} Cells with NA indicate predictor variables that were not included in that model; for instance, focal-partner age interaction and focal-partner admixture score interaction were not included in the Aggregate model, while co-residency with adult daughters and adult maternal sisters were not included in the dyadic index.

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

$$y = X\beta + Zu + e$$

where y is the vector of phenotypic observations, β is the vector of fixed effects, u is the vector of random effects, X and Z are design matrices relating the fixed effects and random effects to each individual and e is the vector of residual errors. We discuss the robustness of this model to the pedigree structure of our population, grooming interactions between kin, and admixture-related variation in genetic ancestry in the [Supplementary Methods](#).

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

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

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

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

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

Heritability of grooming given using the aggregate grooming index

We used the "asremlr" package in Rv.3.0.1 ([Gilmour et al., 2009](#)) to fit a series of linear mixed models with consistent fixed effect structures and increasingly complex random effect structures. We modeled the aggregate grooming behavior of individual i in the following series of nested models:

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

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 random effect of the identity of the focal individual, mom_i is a random effect of the mother of the focal individual, a_{F_i} is the additive genetic contribution of individual i (i.e., its breeding value) and pe_{F_i} represents the “permanent environmental” effect of individual i . Permanent environmental effects represent sources of variance between individuals that arise through environmental effects. We did not include a random effect of year because the aggregate index was standardized across years (see [Supplementary Methods](#)). We used a likelihood ratio test to determine the best-fit model for each grooming index. Including the fixed effects described in Goal 1 could reduce the residual variance reported in our models which may alter our heritability estimates. Therefore, following common practice, we report heritability estimates from models with and without fixed effects (see Results).

Direct and indirect genetic effects on grooming given, using the dyadic grooming index

We next fitted a series of linear mixed models using the dyadic grooming index, again using the “asremlr” package ([Gilmour et al., 2009](#)). The primary benefit of the dyadic grooming index is that it allowed us to investigate indirect genetic effects on grooming, something that is not possible with the aggregate indices.

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

$y_{ijk} = \text{fixed effects} + dyad_{ij} + e_{ijk}$	(null model)
$y_{ijk} = \text{fixed effects} + F_i + dyad_{ij} + e_{ijk}$	(repeatability model)
$y_{ijk} = \text{fixed effects} + F_i + P_j + dyad_{ij} + e_{ijk}$	(repeatability with partner model)
$y_{ijk} = \text{fixed effects} + a_{F_i} + pe_{F_i} + P_j + dyad_{ij} + e_{ijk}$	(direct genetic effects model)
$y_{ijk} = \text{fixed effects} + a_{F_i} + pe_{F_i} + a_{P_j} + pe_{P_j} + dyad_{ij} + e_{ijk}$	(indirect genetic effects model)

where y_{ijk} is the grooming given from individual i to individual j in year, k and $dyad_{ij}$ is an identity assigned to each unique pair of individuals. This term is included because we have repeated measures 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 under Goal 2. P_j is a random effect of the partner individual who received grooming, a_{P_j} is the additive genetic contribution of the individual who received grooming, and pe_{P_j} is the permanent environment effect of the individual who received grooming. The “direct genetic effects” model allows genetic variance among the focal individuals to influence phenotypic variance in grooming given, while the “indirect genetic effects model” allows genetic variance among both the focal and the partner individuals to influence phenotypic variance in grooming given by the focal partner. In the indirect genetic effects model, direct and indirect genetic effects were free to covary, and we estimated the covariance between the direct genetic effects on grooming given (a_{F_i}) and the indirect genetic effects on grooming given (a_{P_j}).

As with Goal 1, because these models are nested with respect to their random effects, we used a likelihood ratio test to determine the best model for the dyadic grooming index.

We also tested models that included random effects of social group and the focal individual’s mother and found no statistically significant variation explained by these effects.

Goal 3: Covariance between DGEs and IGEs, using the dyadic grooming index

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

We also calculated the “total heritability” of our dyadic index of grooming given, following [Bijma et 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 total heritability metric describes the proportion of the variance in grooming given in the dyadic index that is explained by genetic variation in both focal and partner individuals. This metric also takes into account the correlation between IGEs and DGEs, potentially making it a more useful predictor of how a trait shaped by interactions between individuals may respond to selection.

Results

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

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

The environmental predictors of dyadic grooming given were similar to those for aggregate grooming given ([Table 1](#), [Supplementary Table S2](#)). The dominance ranks of the focal female and her partner interacted, such that high-ranking females gave more grooming to high-ranking females than to low-ranking females, and low-ranking females gave more grooming to low-ranking females than to high-ranking females ([Table 1](#), [Supplementary Figure S2](#)). Individuals gave more grooming when their partners were relatives than when their partners were non-relatives and gave more grooming when their partners were their mothers, daughters, or maternal sisters than to other types of partners, even when controlling for relatedness. We also detected a statistically significant effect of group size on the dyadic index, such that females gave less

grooming to each female grooming partner when they were in a larger group; we again note that our analysis may underestimate the strength of this effect (see [Supplementary Methods](#) for details). As with the aggregate index, we found no effect of admixture score on dyadic grooming ([Table 1](#), [Supplementary Table S2](#)).

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

Heritability of aggregate grooming given

The heritability model was the best model for our aggregate index of grooming given, with a heritability estimate of $h^2 = 0.22 \pm 0.048$ ([Table 2](#), [Supplementary Figure S3](#)). This heritability estimate represents the proportion of variance explained by additive genetic variance after conditioning on the fixed effects we included in our model. Conditioning on fixed effects has the potential to significantly affect heritability estimates (see [Methods](#) and [Wilson, 2008](#)). Therefore, we also ran parallel models that excluded fixed effects, which generated very similar heritability estimates ($h^2 = 0.30 \pm 0.07$, [Supplementary Table S3](#)).

Direct and indirect genetic effects on grooming given, using the dyadic index

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

Goal 3: Covariance between DGEs and IGEs

Indirect and direct genetic effects (IGEs and DGEs) for grooming given were strongly positively correlated ($r = 0.74 \pm 0.09$, $p \leq .0001$). To determine if this correlation was significantly different from both 0 and 1, we compare the model in which the correlation between IGEs and DGEs was free to vary (shown in [Table 3](#), last row) with models in which this correlation was constrained to either 0 or 1, using a likelihood ratio test. The model that allowed the genetic correlation to freely vary was the best model and was significantly different from the other two: $p < .0001$ for the comparison with the model in which the covariance was

Table 2. Model comparisons for aggregate grooming given, showing estimates of variance components with standard errors[†] and log-likelihoods (LnL) for each model. *p* values were determined using likelihood ratio tests, with degrees of freedom equal to the number of additional parameters under the more complex model.

Model	σ_A^2	σ_{PE}^2	σ_{mom}^2	σ_F^2	σ_e^2	h^2 ^{††}	LnL	<i>p</i> (versus model one row above)
Null	--	--	--	--	0.728 (0.023)	--	-673.85	--
Repeatability	--	--	--	0.268 (0.033)	0.479 (0.017)	--	-473.60	<0.0001
Maternal effects	--	--	0.091 (0.040)	0.186 (0.037)	0.488 (0.017)	--	-471.23	0.029
Heritability	0.207 (0.065)	0.037 (0.048)	0.045 (0.033)	--	0.488 (0.017)	0.220 (0.048)	-464.22	0.0002

[†] σ_A^2 = additive genetic variance; σ_{PE}^2 = variance attributable to the permanent environment of the focal; σ_{mom}^2 = variance attributable to maternal effects; σ_F^2 = variance attributable to the focal individual, applicable only to the repeatability and maternal effects models that do not include additive genetic effects; σ_e^2 = residual variance.

^{††} Proportion of variance explained by additive genetic variance (σ_A^2).

Table 3. Model comparisons for dyadic grooming given, showing estimates of variance components with standard errors[†] and log-likelihoods (LnL) for each model. *p* values were determined using likelihood ratio tests, with degrees of freedom equal to the number of additional parameters under the more complex model. The indirect genetic effects model allowed the covariance between direct and indirect effects to covary and therefore included two additional parameters over the direct genetic effects model.

Model	$\sigma_{A_f}^2$	$\sigma_{PE_f}^2$	$\sigma_{A_p}^2$	$\sigma_{PE_p}^2$	$\sigma_{E_f}^2$	σ_p^2	σ_{dyad}^2	σ_e^2	DGE ^{††}	IGE [‡]	LnL	<i>p</i> (versus model one row above)
Null	--	--	--	--	--	--	0.211 (0.012)	0.932 (0.012)	--	--	-7263.22	--
Repeatability	--	--	--	--	0.057 (0.008)	--	0.169 (0.010)	0.915 (0.012)	--	--	-7161.53	<0.0001
Repeatability with partner	--	--	--	--	0.059 (0.009)	0.017 (0.004)	0.154 (0.011)	0.911 (0.012)	--	--	-7146.02	<0.0001
Direct genetic effects	0.055 (0.017)	0.010 (0.011)	--	--	--	0.016 (0.004)	0.154 (0.010)	0.911 (0.012)	0.048 (0.015)	--	-7137.37	<0.0001
Indirect genetic effects	0.068 (0.017)	0.007 (0.009)	0.024 (0.006)	4.62e-07 (--) [§]	--	--	0.146 (0.010)	0.914 (0.012)	0.058 (0.014)	0.020 (0.005)	-7114.93	<0.0001

[†] $\sigma_{A_f}^2$ = variance attributable to the additive genetic contribution of the focal; $\sigma_{PE_f}^2$ = variance attributable to the permanent environment of the focal; $\sigma_{A_p}^2$ = variance attributable to the additive genetic contribution of the partner; $\sigma_{PE_p}^2$ = variance attributable to the permanent environment of the partner; $\sigma_{E_f}^2$ = variance attributable to the focal individual, applicable only to the repeatability and maternal effects models that do not include additive genetic effects; σ_p^2 = variance attributable to the partner individual, applicable to the repeatability, maternal effects and DGE models that do not include the additive genetic effects of the partner. σ_{dyad}^2 = variance due to the unique identity of the dyad; σ_e^2 = residual variance.
^{††} Proportion of variance explained by additive genetic variance in focal individuals ($\sigma_{A_f}^2$);
[‡] Proportion of variance explained by additive genetic variance in partner individuals ($\sigma_{A_p}^2$);
[§] With variance component estimates constrained to positive parameter space, no standard error could be estimated for $\sigma_{PE_p}^2$.

constrained to 0, and $p = .006$ for the comparison with the model in which the covariance was constrained to 1. This positive correlation between IGEs and DGEs suggests that specific genetic variants predict increased grooming given by focal individuals, whether those variants are found in the focals themselves or in their grooming partners.

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

Discussion

Here, we provide one of the first empirical estimates of indirect genetic effects on affiliative social behavior in the wild. Our analysis reveals that a focal female's genotype influences the extent to which she grooms her social partners, and her partners' genotypes also appear to influence the focal female's grooming behavior, although this effect is smaller. Furthermore, the genotypes that encourage a female to give grooming to her social partners also may be genotypes that elicit grooming from her social partners. We discuss our main findings below.

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

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

Dominance rank

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

Demographic effects

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

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

We found that the tendency to engage in affiliative social interactions with other females is heritable and consequently, may evolve in response to natural selection. The heritability we detected for aggregate grooming given was 0.22, consistent with heritability estimates reported for life history and behavioral traits in wild populations, but lower than generally reported for morphological traits (Houslay et al., 2021; Visscher et al., 2008). This result provides an important conceptual link between studies that have demonstrated apparent fitness benefits of social interactions and studies that have demonstrated heritability for phenotypes that influence social interactions (e.g., physiology: Insel & Shapiro, 1992; Staes et al., 2018; Walum et al., 2008; personality: Brent et al., 2014; Jang et al., 1996; Moore, 1990; Schielzeth et al., 2012; morphology: Staes et al., 2016). However, further work is needed to predict the magnitude and direction of any response to selection. While we have strong evidence linking grooming behavior to both health (Akinyi et al., 2013) and survival in this study population (Archie et al., 2014; Campos et al., 2020; Silk et al., 2003), we do not yet know whether grooming behavior has a causal link to survival or is simply correlated with other traits that do.

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

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

The total heritability we detected for dyadic grooming given was 0.127. This metric reflects the proportion of variance in dyadic grooming that is explained by genetic effects of both the focal and the partner individual—i.e., direct genetic effects (genetic variation in focal individuals) and indirect genetic effects (genetic variation in partner individuals). It also provides insight into how the relationship between DGEs and IGEs may alter the evolutionary potential of the trait. Although our estimates of IGEs alone were small (0.02 ± 0.005), including them in our model doubled our estimate of the total heritability of dyadic grooming given

compared to a dyadic model that included DGEs alone, because of the positive correlation between IGEs and DGEs for dyadic grooming given. This result is consistent with the expectation that IGEs are an important part of the genetic architecture of grooming given and suggests that grooming behavior may respond to selection more strongly than we would expect from considering DGEs alone. Our results are the first demonstration, to our knowledge, of indirect genetic effects on affiliative social behaviors in a wild vertebrate population. IGEs are thought to be of particular importance in the evolution of social behavior compared to other phenotypes (Bailey et al., 2018; Cheverud, 2003; McGlothlin et al., 2010; Moore et al., 2002; Wolf et al., 1998), and our study stands as an important example of the feasibility of measuring IGEs for social behavior in the wild.

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

An additional strategy for investigating whether the genetic correlation between grooming given and grooming received can be explained by reciprocity would involve trait-based investigations of indirect genetic effects (see Bleakley & Brodie, 2009; McGlothlin & Brodie, 2009; Wolf et al., 1998). Trait-based approaches focus on how phenotypes are influenced by specific traits in a social partner, as opposed to simply estimating the proportion of variance in the focal phenotype explained by similarity in the partner's genotype, as we did here (see also Sartori & Mantovani, 2013; Wilson et al., 2005, 2009, 2011). Our approach, a “variance-partitioning method,” is useful for initial estimates of direct and indirect genetic effects and genetic covariance and is well suited to the genetic structure of our natural breeding population. Future analyses using a trait-based approach would generate further insight into the mechanistic basis of the observed reciprocity. However, a trait-based approach would require fine-grained phenotypic data on the duration and sequential order of grooming bouts, which is not a part of our standard behavioral data collection protocol.

It will be challenging to determine whether the correlation between direct and indirect effects on grooming given does indeed reflect genetic identity between these two apparently

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

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

Future directions

The work described here integrates primate behavioral ecology and quantitative genetics. We hope this integration serves to advance both fields, as behavioral ecology investigates how behavior might evolve in response to ecological and environmental pressures, and quantitative genetics provides the information needed to build realistic evolutionary models that consider the genetic (co)variation in traits (Cheverud & Moore, 1994).

Many previous studies have investigated variation in primate grooming behavior, providing a strong framework for interpreting our results (e.g., Akinyi et al., 2013; Cord, 2012; Dunbar, 1991; Gomes et al., 2009; Keverne et al., 1989; Sánchez-Villagra et al., 1998; Schino & Aureli, 2007; Schino et al., 2009; Silk, 1987, 2007; Wittig et al., 2008). Our study is the first to carry out such an investigation while simultaneously controlling for genetic relatedness between individuals. Our results were broadly consistent with previous studies, with some surprising exceptions that may be due to methodological constraints. For instance, we found that group size affected dyadic grooming, but not aggregate grooming given. This may imply that females adjust their number of grooming partners in response to group size, but

do not adjust the total time spent grooming. Alternatively, aggregate grooming given may be affected by group size in our population and our ability to detect that effect in this study may be reduced by our methodological correction for observer effort. We were also surprised that age and admixture score had no effect on dyadic grooming in our study, as previous work in our population has indicated that younger animals receive more grooming than older animals (Akinyi et al., 2013) and that individuals with higher admixture scores preferentially groom each other (Fogel et al., 2021). However, we note that variance in dyadic grooming explained by either of these parameters may be fully captured by the “dyad” term in our model as the relative ages and admixture scores of partners in a dyad were likely unique to each specific dyad in our study. Our study was designed to investigate the role of genetic variance in grooming behavior; future studies designed to more closely investigate the role of group size, age, and genetic admixture on grooming may shed light on these results.

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

Supplementary material

Supplementary material is available online at *Evolution* (<https://academic.oup.com/evolut/article/77/7/1607/7140279>) by University of Notre Dame user on 05 July 2023

Data availability

The data underlying these analyses are freely available in the Duke University Digital Repository for Research Data. DOI: <http://doi.org/10.7924/r4c252v1k>

Author contributions

E.M.M.: conceptualization, methodology, formal analysis, writing (original draft and review/editing), and funding acquisition. J.A.M.: conceptualization, writing (review/editing). J.T.: resources, data curation, writing (review/editing), and funding acquisition. E.A.A.: resources, data curation, writing (review/editing), and funding acquisition. S.C.A.: conceptualization,

supervision, resources, data curation, writing (review/editing), and funding acquisition.

Funding

We gratefully acknowledge the support of the National Science Foundation (IOS 1456832 to S.C.A. and IOS 1501971 to E.M.M) and the National Institutes of Health (currently through R01AG053308, R01AG053330, R01AG071684, R01HD088558, R01AG075914, and P01AG031719).

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

We thank Duke University, Princeton University, and the University of Notre Dame for financial and logistical support. In Kenya, our research was approved by the Kenya Wildlife Service, the Wildlife Research & Training Institute, the National Environment Management Authority, and the National Council for Science, Technology, and Innovation. We also thank the University of Nairobi, the Institute of Primate Research, the National Museums of Kenya, the members of the Amboseli-Longido pastoralist communities, the Enduimet Wildlife Management Area, Ker & Downey Safaris, Air Kenya, and Safarilink for their cooperation and assistance in the field. Particular thanks go to the Amboseli Baboon Research Project field team (R.S. Mututua, S. Sayialel, J.K. Warutere, I.L. Siodi, G. Marinka, B. Oyath) and camp staff, to T. Wango and V. Oudu for their assistance in Nairobi, and to Jeanne Altmann for her fundamental contributions to the Amboseli baboon research. The baboon project database, BABASE, was designed and programmed by K. Pinc and is managed by N.H. Learn and J.B. Gordon. We thank the three anonymous reviewers and Beniamino Tuliozi for their insightful comments and suggestions which improved this manuscript. **Figure 1** was created with BioRender.com. For a complete set of acknowledgments of funding sources, logistical assistance, and data collection and management, please visit <http://amboselibaboons.nd.edu/acknowledgements/>.

REFERENCES

- Abdellaoui, A., Sanchez-Roige, S., Sealock, J., Treur, J. L., Dennis, J., Fontanillas, P., Elson, S., Nivard, M. G., Ip, H. F., van der Zee, M., Baselmans, B. M. L., Hottenga, J. J., Willemsen, G., Mosing, M., Lu, Y., Pedersen, N. L., Denys, D., Amin, N., van Duijn, C. M., & Boomsma, D. I.; 23andme Research Team (2019). Phenome-wide investigation of health outcomes associated with genetic predisposition to loneliness. *Human Molecular Genetics*, 28, 3853–3865.
- Akinyi, M. Y., Tung, J., Jeneby, M., Patel, N. B., Altmann, J., & Alberts, S. C. (2013). Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, 85(3), 559–568. <https://doi.org/10.1016/j.anbehav.2012.12.012>
- Alberts, S., & Altmann, J. (2012). The Amboseli Baboon research project: 40 years of continuity and change. In P. Kappeler, & D. Watts (Eds.), *Long-term field studies of primates* (pp. 261–288). Springer Verlag.
- Alberts, S. C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, 88, 47–66.
- Alberts, S. C., & Altmann, J. (2001). Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology*, 53(4), 139–154. <https://doi.org/10.1002/ajp.1>
- Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From mating opportunities to paternity success. *Animal Behaviour*, 72(5), 1177–1196. <https://doi.org/10.1016/j.anbehav.2006.05.001>
- Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings Biological Sciences*, 281(1793), 20141261. <https://doi.org/10.1098/rspb.2014.1261>
- Ashbrook, D. G., Gini, B., & Hager, R. (2015). Genetic variation in offspring indirectly influences the quality of maternal behaviour in mice. *eLife*, 4, e11814. <https://doi.org/10.7554/eLife.11814>
- Bailey, N. W., Marie-Orleach, L., & Moore, A. J. (2018). Indirect genetic effects in behavioral ecology: Does behavior play a special role in evolution?. *Behavioral Ecology*, 29, 1–11.
- Baud, A., McPeck, S., Chen, N., & Hughes, K. A. (2022). Indirect genetic effects: A cross-disciplinary perspective on empirical studies. *Journal of Heredity*, 113, 1–15.
- Bijma, P., Muir, W. M., & Van Arendonk, J. A. M. (2007). Multilevel selection 1: Quantitative genetics of inheritance and response to selection. *Genetics*, 175(1), 277–288. <https://doi.org/10.1534/genetics.106.062711>
- Bijma, P., & Wade, M. J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology*, 21(5), 1175–1188. <https://doi.org/10.1111/j.1420-9101.2008.01550.x>
- Bleakley, B. H., & Brodie, E. D. III (2009). Indirect genetic effects influence antipredator behavior in guppies: Estimates of the coefficient of interaction Psi and the inheritance of reciprocity. *Evolution*, 63, 1796–1806.
- Blomquist, G. E., & Brent, L. J. N. (2014). Applying quantitative genetic methods to primate social behavior. *International Journal of Primatology*, 35, 108–128.
- Brent, L. J. N., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., Skene, J. H. P., & Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports*, 3, 1042.
- Brent, L. J. N., Semple, S., Maclarnon, A., Ruiz-Lambides, A., Gonzalez-Martinez, J., & Platt, M. L. (2014). Personality traits in Rhesus Macaques (*Macaca mulatta*) are heritable but do not predict reproductive output. *International Journal of Primatology*, 35, 188–209.
- Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature*, 425(6954), 179–181. <https://doi.org/10.1038/nature01866>
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, 106, 13850–13853.
- Campos, F. A., Archie, E. A., Gesquiere, L. R., Tung, J., Altmann, J., & Alberts, S. C. (2021). Glucocorticoid exposure predicts survival in female baboons. *Science Advances*, 7(17), eabf6759. <https://doi.org/10.1126/sciadv.abf6759>
- Campos, F. A., Villavicencio, F., Archie, E. A., Colchero, F., & Alberts, S. C. (2020). Social bonds, social status and survival in wild baboons: A tale of two sexes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1811), 20190621. <https://doi.org/10.1098/rstb.2019.0621>
- Charpentier, M. J. E., Tung, J., Altmann, J., & Alberts, S. C. (2008). Age at maturity in wild baboons: Genetic, environmental and demographic influences. *Molecular Ecology*, 17(8), 2026–2040. <https://doi.org/10.1111/j.1365-294X.2008.03724.x>
- Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2012). Evidence for intra-sexual selection in wild female baboons. *Animal Behaviour*, 84(1), 21–27. <https://doi.org/10.1016/j.anbehav.2012.03.010>

- Cheverud, J. M. (2003). Evolution in a genetically heritable social environment. *Proceedings of the National Academy of Sciences*, 100, 4357–4359.
- Cheverud, J., & Moore, A. (1994). Quantitative genetics and the role of the environment provided by relatives in behavioral evolution. In C. Boake (Ed.), *Quantitative genetic studies of behavioral evolution* (pp. 67–100). University of Chicago Press.
- Cords, M. (2012). The behavior, ecology and social evolution of cercopithecine monkeys. In J. Mitani, J. Call, P. Kappeler, R. Palombit, & J. Silk (Eds.), *The evolution of primate societies* (pp. 91–112). University of Chicago Press.
- Darlington, R. B., & Smulders, T. V. (2001). Problems with residual analysis. *Animal Behaviour*, 62(3), 599–602. <https://doi.org/10.1006/anbe.2001.1806>
- Day, F. R., Ong, K. K., & Perry, J. R. B. (2018). Elucidating the genetic basis of social interaction and isolation. *Nature Communications*, 9(1), 2457. <https://doi.org/10.1038/s41467-018-04930-1>
- Díaz-Muñoz, S. L., DuVal, E. H., Krakauer, A. H., & Lacey, E. A. (2014). Cooperating to compete: Altruism, sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, 88, 67–78. <https://doi.org/10.1016/j.anbehav.2013.11.008>
- Dunbar, R. I. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121–131.
- Dunbar, R. I. M., & Sharman, M. (1984). Is social grooming altruistic?. *Zeitschrift für Tierpsychologie*, 64, 163–173.
- Edwards, A. C., Rollmann, S. M., Morgan, T. J., & Mackay, T. F. C. (2006). Quantitative genomics of aggressive behavior in *Drosophila melanogaster*. *PLoS Genetics*, 2, e154.
- Ellis, S., Franks, D. W., Natrass, S., Cant, M. A., Weiss, M. N., Giles, D., Balcomb, K. C., & Croft, D. P. (2017). Mortality risk and social network position in resident killer whales: Sex differences and the importance of resource abundance. *Proceedings of the Royal Society B: Biological Sciences*, 284(1865), 20171313. <https://doi.org/10.1098/rspb.2017.1313>
- Ezenwa, V. O., Ghai, R. R., McKay, A. F., & Williams, A. E. (2016). Group living and pathogen infection revisited. *Current Opinion in Behavioral Sciences*, 12, 66–72. <https://doi.org/10.1016/j.cobeha.2016.09.006>
- Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *iScience*, 24(8), 102864. <https://doi.org/10.1016/j.isci.2021.102864>
- Fisher, D. N. (2023). Direct and indirect phenotypic effects on sociability indicate potential to evolve. *Journal of Evolutionary Biology*, 36(1), 209–220. <https://doi.org/10.1111/jeb.14110>
- Fogel, A. S., McLean, E. M., Gordon, J. B., Archie, E. A., Tung, J., & Alberts, S. C. (2021). Genetic ancestry predicts male–female affiliation in a natural baboon hybrid zone. *Animal Behaviour*, 180, 249–268. <https://doi.org/10.1016/j.anbehav.2021.07.009>
- Foster, K. R., Shaulsky, G., Strassmann, J. E., Queller, D. C., & Thompson, C. R. L. (2004). Pleiotropy as a mechanism to stabilize cooperation. *Nature*, 431(7009), 693–696. <https://doi.org/10.1038/nature02894>
- Fowler, J. H., Dawes, C. T., & Christakis, N. A. (2009). Model of genetic variation in human social networks. *Proceedings of the National Academy of Sciences*, 106(6), 1720–1724. <https://doi.org/10.1073/pnas.0806746106>
- Franz, M., McLean, E., Tung, J., Altmann, J., & Alberts, S. C. (2015). Self-organizing dominance hierarchies in a wild primate population. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151512. <https://doi.org/10.1098/rspb.2015.1512>
- Galezo, A. A., Nolas, M. A., Fogel, A. S., Mututua, R. S., Warutere, J. K., Siodi, I. L., Altmann, J., Archie, E. A., Tung, J., & Alberts, S. C. (2022). Mechanisms of inbreeding avoidance in a wild primate. *Current Biology*, 32(7), 1607–1615.e4. <https://doi.org/10.1016/j.cub.2022.01.082>
- Gauzere, J., Pemberton, J. M., Morris, S., Morris, A., Kruuk, L. E. B., & Walling, C. A. (2020). The genetic architecture of maternal effects across ontogeny in the red deer. *Evolution*, 74(7), 1378–1391. <https://doi.org/10.1111/evo.14000>
- Gilmour, A., B. Cullis, R. Thompson, W. Street, and H. Hempstead. 2009. *ASReml Update*. What's new in Release 3.00. Hemel Hempstead, UK: VSN International.
- Godoy, I., Korsten, P., & Perry, S. E. (2022). Genetic, maternal, and environmental influences on sociality in a pedigreed primate population. *Heredity*, 129(4), 203–214. <https://doi.org/10.1038/s41437-022-00558-6>
- Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 276(1657), 699–706. <https://doi.org/10.1098/rspb.2008.1324>
- Griffin, A. S., West, S. A., & Buckling, A. (2004). Cooperation and competition in pathogenic bacteria. *Nature*, 430(7003), 1024–1027. <https://doi.org/10.1038/nature02744>
- Henzi, S. P., Lycett, J. E., & Weingrill, T. (1997). Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour*, 54(5), 1235–1243. <https://doi.org/10.1006/anbe.1997.0520>
- Holt-Lunstad, J., Smith, T. B., Baker, M., Harris, T., & Stephenson, D. (2015). Loneliness and social isolation as risk factors for mortality: A meta-analytic review. *Perspectives on Psychological Science*, 10(2), 227–237. <https://doi.org/10.1177/1745691614568352>
- Houslay, T. M., Nielsen, J. F., & Clutton-Brock, T. H. (2021). Contributions of genetic and nongenetic sources to variation in cooperative behavior in a cooperative mammal. *Evolution*, 75(3071), 3086.
- Hunt, J., & Simmons, L. W. (2002). The genetics of maternal care: Direct and indirect genetic effects on phenotype in the dung beetle *Onthophagus taurus*. *Proceedings of the National Academy of Sciences*, 99(10), 6828–6832. <https://doi.org/10.1073/pnas.092676199>
- Insel, T. R., & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences of the United States of America*, 89(13), 5981–5985. <https://doi.org/10.1073/pnas.89.13.5981>
- Jang, K. L., Livesley, W. J., & Vernon, P. A. (1996). Heritability of the big five personality dimensions and their facets: A twin study. *Journal of Personality*, 64(3), 577–591. <https://doi.org/10.1111/j.1467-6494.1996.tb00522.x>
- Kasper, C., Kölliker, M., Postma, E., & Taborsky, B. (2017). Consistent cooperation in a cichlid fish is caused by maternal and developmental effects rather than heritable genetic variation. *Proceedings of the Royal Society B: Biological Sciences*, 284(1858), 20170369. <https://doi.org/10.1098/rspb.2017.0369>
- Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, 14(1-2), 155–161. [https://doi.org/10.1016/0306-4530\(89\)90065-6](https://doi.org/10.1016/0306-4530(89)90065-6)
- Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the “animal model”. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 873–890.
- Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology*, 20(5), 1890–1903. <https://doi.org/10.1111/j.1420-9101.2007.01377.x>
- Lea, A. J., Blumstein, D. T., Wey, T. W., & Martin, J. G. A. (2010). Heritable victimization and the benefits of agonistic relationships. *Proceedings of the National Academy of Sciences*, 107, 21587–21592.
- Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour*, 74, 1617–1629.
- Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sinauer Associates.
- McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, 9(4), 20130428. <https://doi.org/10.1098/rsbl.2013.0428>
- McFarlane, S. E., Gorrell, J. C., Coltman, D. W., Humphries, M. M., Boutin, S., & McAdam, A. G. (2015). The nature of nurture in a wild mammal's fitness. *Proceedings of the Royal Society B: Biological*

- Sciences*, 282(1806), 20142422. <https://doi.org/10.1098/rspb.2014.2422>
- McGlothlin, J. W., & Brodie, E. D. III (2009). How to measure indirect genetic effects: The congruence of trait-based and variance-partitioning approaches. *Evolution*, 63(7), 1785–1795. <https://doi.org/10.1111/j.1558-5646.2009.00676.x>
- McGlothlin, J. W., Moore, A. J., Wolf, J. B., & Brodie III, E. D. (2010). Interacting phenotypes and the evolutionary process: III Social evolution. *Evolution*, 64(9), 2558–2574. <https://doi.org/10.1111/j.1558-5646.2010.01012.x>
- Moore, A. J. (1990). The inheritance of social dominance, mating behaviour and attractiveness to mates in male *Nauphoeta cinerea*. *Animal Behaviour*, 39(2), 388–397. [https://doi.org/10.1016/s0003-3472\(05\)80886-3](https://doi.org/10.1016/s0003-3472(05)80886-3)
- Moore, A. J., Haynes, K. F., Preziosi, R. F., & Moore, P. J. (2002). The evolution of interacting phenotypes: Genetics and evolution of social dominance. *The American Naturalist*, 160(Suppl 6), S186–S197. <https://doi.org/10.1086/342899>
- Moore, A. J., Brodie, E. D. III, & Wolf, J. B. (1997). Interacting phenotypes and the evolutionary process: I Direct and indirect genetic effects of social interactions. *Evolution*, 51, 1352–1362.
- Nakamichi, M. (2003). Age-related differences in social grooming among adult female Japanese monkeys (*Macaca fuscata*). *Primates*, 44(3), 239–246. <https://doi.org/10.1007/s10329-003-0036-x>
- Rainey, P. B., & Rainey, K. (2003). Evolution of cooperation and conflict in experimental bacterial populations. *Nature*, 425(6953), 72–74. <https://doi.org/10.1038/nature01906>
- Saltz, J. B. (2013). Genetic composition of social groups influences male aggressive behaviour and fitness in natural genotypes of *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences*, 280(1771), 20131926. <https://doi.org/10.1098/rspb.2013.1926>
- Sánchez-Villagra, M. R., Pope, T. R., & Salas, V. (1998). Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). *International Journal of Primatology*, 19, 473–491.
- Santostefano, F., Allegue, H., Garant, D., Bergeron, P., & Réale, D. (2021). Indirect genetic and environmental effects on behaviors, morphology, and life-history traits in a wild Eastern chipmunk population. *Evolution*, 75(6), 1492–1512. <https://doi.org/10.1111/evo.14232>
- Sartori, C., & Mantovani, R. (2013). Indirect genetic effects and the genetic bases of social dominance: Evidence from cattle. *Heredity*, 110(1), 3–9. <https://doi.org/10.1038/hdy.2012.56>
- Saunders, C. D., & Hausfater, G. (1988). The functional significance of baboon grooming behavior. *Annals of the New York Academy of Sciences*, 525(1 Neural Mechan), 430–432. <https://doi.org/10.1111/j.1749-6632.1988.tb38635.x>
- Schielzeth, H., Kempenaers, B., Ellegren, H., & Forstmeier, W. (2012). QTL linkage mapping of zebra finch beak color shows an oligogenic control of a sexually selected trait. *Evolution*, 66(1), 18–30. <https://doi.org/10.1111/j.1558-5646.2011.01431.x>
- Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18, 115–120.
- Schino, G. (2001). Grooming, competition and social rank among female primates: A meta-analysis. *Animal Behaviour*, 62(2), 265–271. <https://doi.org/10.1006/anbe.2001.1750>
- Schino, G., & Aureli, F. (2007). Grooming reciprocation among female primates: A meta-analysis. *Biology Letters*, 4(1), 9–11. <https://doi.org/10.1098/rsbl.2007.0506>
- Schino, G., Di Giuseppe, F., & Visalberghi, E. (2009). Grooming, rank, and agonistic support in tufted capuchin monkeys. *American Journal of Primatology*, 71(2), 101–105. <https://doi.org/10.1002/ajp.20627>
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698. [https://doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/10.1016/0022-5193(77)90015-7)
- Silk, J. (1987). Social behavior in evolutionary perspective. In B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. Struhsaker (Eds.), *Primate societies* (pp. 318–329). University of Chicago Press.
- Silk, J. B. (2007). Social components of fitness in primate groups. *Science*, 317(5843), 1347–1351. <https://doi.org/10.1126/science.1140734>
- Silk, J. B. (2002). The form and function of reconciliation in primates. *Annual Review of Anthropology*, 31(1), 21–44. <https://doi.org/10.1146/annurev.anthro.31.032902.101743>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302(5648), 1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavior, Ecology and Sociobiology*, 61(2), 197–204. <https://doi.org/10.1007/s00265-006-0250-9>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>
- Silk, J., & Frank, R. (2009). Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons. *Behaviour*, 146(8), 1123–1135. <https://doi.org/10.1163/156853909x406455>
- Springer, S. A., Crespi, B. J., & Swanson, W. J. (2011). Beyond the phenotypic gambit: Molecular behavioural ecology and the evolution of genetic architecture. *Molecular Ecology*, 20(11), 2240–2257. <https://doi.org/10.1111/j.1365-294X.2011.05116.x>
- Staes, N., Bradley, B. J., Hopkins, W. D., & Sherwood, C. C. (2018). Genetic signatures of socio-communicative abilities in primates. *Current Opinion in Behavioral Sciences*, 21, 33–38. <https://doi.org/10.1016/j.cobeha.2017.11.013>
- Staes, N., Weiss, A., Helsen, P., Korody, M., Eens, M., & Stevens, J. M. G. (2016). Bonobo personality traits are heritable and associated with vasopressin receptor gene 1a variation. *Scientific Reports*, 6, 38193. <https://doi.org/10.1038/srep38193>
- Stanton, M. A., & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One*, 7(10), e47508. <https://doi.org/10.1371/journal.pone.0047508>
- Strassmann, J. E., Zhu, Y., & Queller, D. C. (2000). Altruism and social cheating in the social amoeba *Dictyostelium discoideum*. *Nature*, 408(6815), 965–967. <https://doi.org/10.1038/35050087>
- Tanaka, I., & Takefushi, H. (1993). Elimination of external parasites (Lice) is the primary function of grooming in free-ranging Japanese Macaques. *Anthropological Science*, 101(2), 187–193. <https://doi.org/10.1537/ase.101.187>
- Thompson, N. A., & Cords, M. (2018). Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecology and Evolution*, 8(3), 1604–1614. <https://doi.org/10.1002/ece3.3781>
- Tung, J., Charpentier, M. J. E., Garfield, D. A., Altmann, J., & Alberts, S. C. (2008). Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. *Molecular Ecology*, 17(8), 1998–2011. <https://doi.org/10.1111/j.1365-294X.2008.03723.x>
- Tung, J., Charpentier, M. J., Mukherjee, S., Altmann, J., & Alberts, S. C. (2012). Genetic effects on mating success and partner choice in a social mammal. *American Naturalist*, 180(1), 113–129. <https://doi.org/10.1086/665993>
- Van Horn, R. C., Buchan, J. C., Altmann, J., & Alberts, S. C. (2007). Divided destinies: Group choice by female savannah baboons during social group fission. *Behavior, Ecology and Sociobiology*, 61(12), 1823–1837. <https://doi.org/10.1007/s00265-007-0415-1>
- Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D. W., & Pelletier, F. (2015). Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. *Ecology*, 96(3), 631–641. <https://doi.org/10.1890/14-1320.1>

- Vilgalys, T. P., Fogel, A. S., Anderson, J. A., Mututua, R. S., Warutere, J. K., Siodi, I. L., Kim, S. Y., Voyles, T. N., Robinson, J. A., Wall, J. D., Archie, E. A., Alberts, S. C., & Tung, J. (2022). Selection against admixture and gene regulatory divergence in a long-term primate field study. *Science*, 377(6606), 635–641. <https://doi.org/10.1126/science.abm4917>
- Visscher, P. M., Hill, W. G., & Wray, N. R. (2008). Heritability in the genomics era—Concepts and misconceptions. *Nature Reviews Genetics*, 9(4), 255–266. <https://doi.org/10.1038/nrg2322>
- Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J. M., Reiss, D., Igl, W., Ganiban, J. M., Spotts, E. L., Pedersen, N. L., Eriksson, E., & Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. *Proceedings of the National Academy of Sciences*, 105, 14153–14156.
- Wice, E. W., & Saltz, J. B. (2023). Indirect genetic effects for social network structure in *Drosophila melanogaster*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378(1874), 20220075. <https://doi.org/10.1098/rstb.2022.0075>
- Wilson, A. J. (2008). Why h^2 does not always equal V_A/V_P ?. *Journal of Evolutionary Biology*, 21(3), 647–650. <https://doi.org/10.1111/j.1420-9101.2008.01500.x>
- Wilson, A. J., Coltman, D. W., Pemberton, J. M., Overall, A. D. J., Byrne, K. A., & Kruuk, L. E. B. (2005). Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *Journal of Evolutionary Biology*, 18(2), 405–414. <https://doi.org/10.1111/j.1420-9101.2004.00824.x>
- Wilson, A. J., Gelin, U., Perron, M. -C., & Réale, D. (2009). Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proceedings Biological Sciences*, 276(1656), 533–541. <https://doi.org/10.1098/rspb.2008.1193>
- Wilson, A. J., Morrissey, M. B., Adams, M. J., Walling, C. A., Guinness, F. E., Pemberton, J. M., Clutton-Brock, T. H., & Kruuk, L. E. B. (2011). Indirect genetics effects and evolutionary constraint: An analysis of social dominance in red deer, *Cervus elaphus*. *Journal of Evolutionary Biology*, 24(4), 772–783. <https://doi.org/10.1111/j.1420-9101.2010.02212.x>
- Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, 54(1), 170–177. <https://doi.org/10.1016/j.yhbeh.2008.02.009>
- Wolf, J. B., Brodie, E. D., III Cheverud, J. M., Moore, A. J., & Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution*, 13(2), 64–69. [https://doi.org/10.1016/s0169-5347\(97\)01233-0](https://doi.org/10.1016/s0169-5347(97)01233-0)
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75(3-4), 262–300. <https://doi.org/10.1163/156853980x00447>
- Xavier, J. B., & Foster, K. R. (2007). Cooperation and conflict in microbial biofilms. *Proceedings of the National Academy of Sciences*, 104, 876–881.
- Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the National Academy of Sciences*, 111, 18195–18200.