Social and genetic interactions drive fitness variation in a free-living dolphin population

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The evolutionary forces that drive fitness variation in species are of considerable interest. Despite this, the relative importance and interactions of genetic and social factors involved in the evolution of fitness traits in wild mammalian populations are largely unknown. To date, a few studies have demonstrated that fitness might be influenced by either social factors or genes in natural populations, but none have explored how the combined effect of social and genetic parameters might interact to influence fitness. Drawing from a long-term study of wild bottlenose dolphins in the eastern gulf of Shark Bay, Western Australia, we present a unique approach to understanding these interactions. Our study shows that female calving success depends on both genetic inheritance and social bonds. Moreover, we demonstrate that interactions between social and genetic factors also influence female fitness. Therefore, our study represents a major methodological advance, and provides critical insights into the interplay of genetic and social parameters of fitness.

animal model | gene-culture coevolution | social learning | reproductive success | relatedness

The reproductive consequences of sociality in mammalian-societies attract substantial interest. Although a few studies have demonstrated a direct link between social parameters and fitness (1–3), our knowledge about how social relationships might drive fitness variation still remains incomplete (4). In particular, the ways in which social and genetic parameters might interact to influence fitness variation in wild mammalian populations has, to date, received no attention. This gap is partially due to the difficulties associated with data collection as well as the lack of analytic techniques for partitioning social and genetic effects and for examining interactions. The methodology presented here addresses this gap. We present evidence that, in species characterized by complex social systems, individual variation in fitness may be best understood by investigating the influence of genetic heritability and social associations upon those traits, and the interactions of genes and sociality.

The genetic heritability of fitness traits has been widely examined in both experimental settings (5) and free-ranging populations (6–8). However, in species characterized by slow life histories, extended maternal care, and complex sociality (e.g., primates, elephants, small delphinids), individual variation in fitness traits might be best understood when also accounting for an individual's behavioral context, such as their common associates or group membership. In cases in which social transmission of information occurs, the fitness of social learners can be dependent upon the individuals from whom they acquire information or from whom they learn (9, 10). Only a few studies have investigated the correlation between shared group membership or close association and fitness traits (2, 3). For instance, in female feral horses (*Equus caballus*), social integration between unrelated females was shown to increase both foal birth rates and survival, independent of maternal habitat quality, social group type, dominance status, and age (1). Yet, in wild populations, genetic heritability and the social components of fitness have not been examined together.

Characterized by complex cognitive abilities and a highly intricate social system, bottlenose dolphins (*Tursiops* sp.) are prime candidates for investigating how genetic and social parameters may affect fitness. Like the great apes (11, 12), bottlenose dolphins have slow life histories characterized by late sexual maturity, long interbirth intervals, and extensive maternal care (13, 14). In the eastern gulf of Shark Bay, Western Australia, bottlenose dolphins have been the focus of extensive study since the mid-1980s (15), making them one of the most comprehensively studied dolphin populations in the world. This population of bottlenose dolphins exhibits an elaborate social system, with some characteristics, such as multilevel male alliances within social groups, that are otherwise found only in humans (16). Adult males and females are generally found in separate groups within an open fission–fusion social system (15), in which group composition and size frequently change (15). Social learning has also been documented in this population (17, 18). All females in the study population were recognizable, and their survival and reproductive rates have been monitored (13). We focused on life history data from 52 female bottlenose dolphins in this population.

We explored the genetic and social effects on a partial measure of fitness, namely, female calving success (Cs), using a pedigree-free animal model (19). This recently developed pedigree-free animal model uses a matrix of pairwise genetic relatedness, rather than pedigree information, to assess the heritability and genetic variance of complex traits in wild populations (19). To make a comparable investigation of genetic and social factors, we developed this method further by using two measures for each pair of females: pairwise genetic relatedness (Queller and Goodnight measure, ref. 20) and a measure of sociality based on pairwise association [half weight index (HWI), ref. 21]. We also examined whether genetic heritability and social effects interact in their effects on female Cs.

Results

The animal model showed that both additive genetic variance ($A\text{-}G_V$) and additive social variance ($A\text{-}S_V$) were significantly different from zero (Table 1, for $A\text{-}G_V$ $0.001 < P \leq 0.032$, for $A\text{-}S_V$ $0.001 < P \leq 0.028$) and were robust to removal of single individuals (Table S3). Thus, $A\text{-}G_V$ and $A\text{-}S_V$ are both significant predictors of female fitness. Additive genetic variance accounted for 16.2% of the variation in female Cs ($h^2_G = 0.162$, Table 1), whereas additive social variance accounted for 44% of the var-

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Table 1. Genetic and social effects on the fitness trait "calving success" in female bottlenose dolphins, using a pedigree-free animal model

Effect	Additive variance	Residual	h^2	Coefficient of additive variance	Null LRT *P*	Const LRT*P*	Random *P*
Genetic effect	A-G_V = 0.005 (± 0.002)	A-G_R = 0.026 (± 0.02)	h^2_G = 0.162	(CV_A-*G*) = 48.43	**0.032**	**<0.001***	**0.03**
Social effect	A-S_V = 0.007 (± 0.003)	A-S_R = 0.009 (± 0.025)	h^2_S = 0.44	(CV_A-*S*) = 57.3	**0.028**	**<0.001**[†]	**0.02**

Table shows additive genetic variance (A-G_V), residuals (A-G_R), genetic heritability (h^2_G), and coefficient of additive genetic variance (CV_A-*G*). In brackets are the SEs. Three tests for significance were conducted, which are detailed in *Materials and Methods*: a null log-likelihood ratio test of the additive variances (Null LRT), a constrained log-likelihood ratio test of the additive variances (Const LRT), and a randomization procedure test of the h^2 values (Random). Females' identity was added to the model as fixed effect. To account for heterogeneity of number of records per female, the pedigree-free animal model was weighted by the number of years for which each female was monitored. When the relatedness matrix is replaced by the social association (HWI) matrix, A-S_V, A-S_R, h^2_S and (CV_A-*S*) are the equivalent statistics for social effects on Cs.

*Cons-LRT-Genetic Effect: − 2× difference in log-likelihood between unconstrained model (our full model) and constrained model (A-G_V variance set to zero) = 10.8, χ^2_1 = 10.8, $P < 0.001$.

[†]Cons-LRT-Social Effect: − 2× difference in log-likelihood between unconstrained model (our full model) and constrained model (A-S_V variance set to zero) = 12.2, χ^2_1 = 12.2, $P < 0.001$.

iation in female Cs (h^2_S = 0.44, Table 1). A randomization test showed that the heritability estimates were significantly different from random expectations ("Random" in Table 1, for A-G_V $P \leq$ 0.03, for A-S_V $P \leq$ 0.02).

Current animal models cannot incorporate multiple matrices as predicting variables, and therefore cannot be used to investigate interactions between predictors. To investigate how genetic relationships and social associations between individuals might correlate and/or interact in their effects on Cs, we therefore used two alternative approaches. First, we measured breeding values. In this study, a female's breeding value for Cs is the total additive effect of her genes on Cs. For the social analysis, a female's breeding value shows the effects of social interactions on her Cs. The animal model was used to generate best linear unbiased predictors (BLUPs) to estimate, for each female, the genetic breeding value (G-EBV) and social breeding value (S-EBV) of female Cs (Cs), and found that they were indeed positively correlated ($P = 0.0001$; Fig. 1). Second, we used generalized linear mixed models (GLMM) to investigate whether a female's Cs correlates with the Cs of her close relatives (genetic effect) and preferred associates (social effect) and whether there was an interaction between these two effects. We found that the mean Cs of a female's close relatives (genetic effect) and the mean Cs of her preferred associates (social effect) showed a significant multiplicative interaction in their effect on Cs (Table 2 and Fig. 2). The significance of the multiplicative genetic and social interaction on Cs was also confirmed when compared with a null model with no interaction (Wald test: df = 51, χ^2 = −3 118.33, $P < 2.2e\text{-}16$). In addition, we compared this model to three other models that did not include the genetic and social interaction; in all three cases, the models showed higher Akaike information coefficient values, that is, poorer fit (Table S1). The inclusion of the interaction of social and genetic effects in the GLMM model led to the nonsignificance of the individual factors (genetic or social) (Table 2). To visually display the nature of the significant interaction of the genetic and social effects on Cs, we separated the Cs of preferred associates (social effect) into pairs of females with low relatedness (Fig. 2, squares) and pairs of females with high relatedness (Fig. 2, circles). In particular, we found that the social effect (extent of fitness of preferred associates) was more important for female pairs with low relatedness than for female pairs with high relatedness (Fig. 2).

Last, we did not find correlations between Cs and the extent of relatedness of preferred associates, the amount of time that a female spends in social groups, the size of her home range, or the interactions of these variables (Table S2).

Discussion

Our approach offers insights into the adaptive value of sociality in mammalian societies. We show that both heritable genetic and social factors contribute to the variation of a fitness trait in a wild

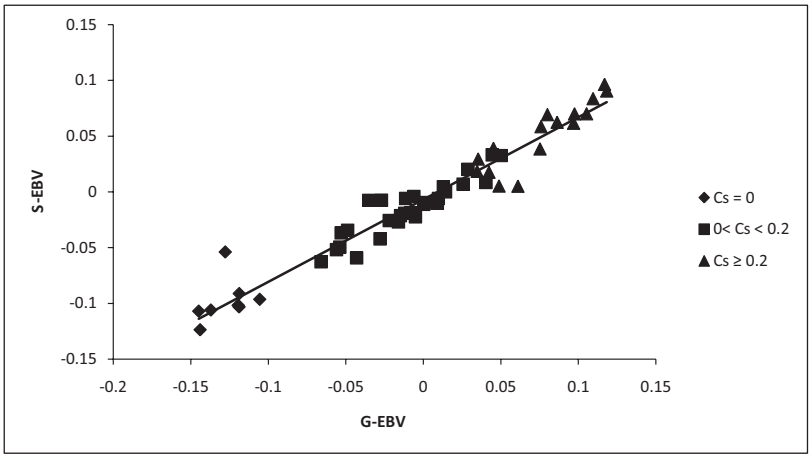

Fig. 1. Significant regression of social (S-EBV) on genetic (G-EBV) breeding values (BLUP) of female Cs. Vertical axis shows S-EBV, the additive social effects on Cs for each female, and the horizontal axis shows G-EBV, the additive genetic effect on the Cs of the same female. Triangles represent females with high fitness (Cs ≥ 0.2; $n = 16$); squares represent females with medium fitness (0 < Cs < 0.2; $n = 28$); and diamonds represent females with low fitness (Cs = 0; $n = 8$). (S-EBV) = −0.006 + 0.74(G-EBV), adjusted $R^2 = 0.94$, $F_{1,50} = 859.71$, $P < 0.0001$.

Table 2. Predictors of female Cs (n = 52)

Model	Average effect	SE	t	df	P
Cs ∝ MCs_{-PA} + MCs_{-CR} + MCs_{-PA}: MCs_{-CR}					
MCs_{-PA}	−3.75	2.69	−1.41	48	0.164
MCs_{-CR}	−4.35	2.55	−1.70	48	0.095
MCs_{-PA}: MCS_{-CR}	38.14	15.43	2.47	48	**0.0171**

GLMM model assumed a binomial distribution and was weighted by number of years for which each female was monitored. Female identity was added as random effect. Explanatory factors are mean Cs of a female's preferred associates (MCs_{-PA}), mean Cs of a female's close relatives (MCs_{-CR}), and their multiplicative interactions (MCs_{-PA}: MCs_{-CR}). Wald test: df = 51, χ^2 = −3 118.33, P < 2.2e-16. Bold indicates significant P values.

population. The social effect is consistent with either social transmission of reproductive prowess, or with the suggestion that females with calves associate with other females with calves (22), a type of homophily. For instance, females with calves might attract other females with calves during times of high predation pressure (23, 24) to lower the requirement for individual vigilance (e.g., kangaroos; 25) or for other social benefits. Furthermore, the social effect provides evidence for the hypothesis that social effects can drive phenotypic evolution whenever the phenotype of one individual influences the phenotype or fitness of a conspecific (26–28).

Although we understand that there are concerns about using BLUPs (29), the individual breeding values that they generate comprise, to date, the only identifiable method that allows us to directly investigate how two pedigree-free animal models might correlate in their effects on a phenotypic trait. Moreover, the BLUP analysis was confirmed by an independent analysis (GLMM, Table 2), which also identified the significant interaction between genetic and social effects (Table 2). The two analyses are in agreement, together providing evidence that social and genetic factors have a significant effect, with interaction in their effects on Cs. Pairs of females that are closely related have similar fitness, and pairs of females that preferentially associate also have similar fitness. Although this pattern might simply result from preferential association of close relatives, this is not the case for the three following reasons. First, it is important to note that the pairs of females that are closely related might not be the same pairs as those that preferentially associate with each other. This was confirmed by Frère et al. (30), who showed that the social and relatedness matrices were only very weakly correlated (r < 0.06) in this population. This indicates that females' associates include individuals other than close relatives. Second, the social and genetic GLMM analysis further emphasizes that the relationship between the genetic and social effect on fitness is not simply collinear, but that the genetic and social effects interact to influence fitness. In other words, this means that the genetic and social effects on fitness are not simply additive. Last, we did not find that preferentially associating with close relatives resulted in high Cs (Table S2).

We also investigated possible alternative explanations for the patterns that we observed. In particular, we investigated whether high Cs could be a function of either the amount of time that a female spends in social groups or the size of her home range, but we found that neither of these effects was significant (Table S2). This is not to say that the environment does not influence reproduction, because females that tend to preferentially associate also overlap in home range (30). This relationship found between female–female association patterns and home range overlap in our study population highlights the fact that the social matrix also contains critical environmental information. This overlay of social and environmental information within the social matrix might be part of the reason for the high h^2_S estimate (44%). For instance, water depth was found to predict female reproductive success in our study population, possibly because females found in shallow water may benefit from higher prey density (31). In addition, other parameters, such as age and previous breeding experience, were also found to affect female reproductive success in other marine mammals (32–34).

Although a few studies have demonstrated that fitness might be influenced by either sociality or genes in natural populations, none have explored how the combined effect of social and genetic parameters might interact to influence fitness. By extending the pedigree-free animal model, this study presents a unique attempt to investigate such interactions. We demonstrate not only that a female fitness trait is influenced by both genetic and social effects, but that these effects on the evolution of fitness traits are strongly intertwined (35–37).

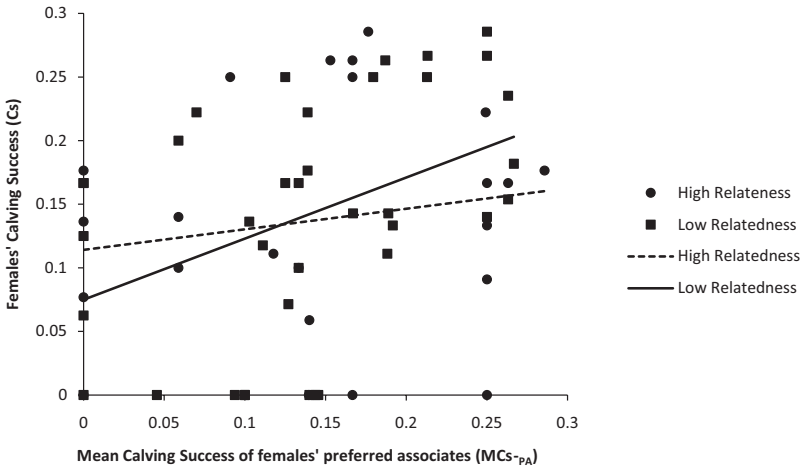

Fig. 2. Visual representation of significant multiplicative interactions between social and genetic effects on females' Cs identified in Table 2. Each point represents a single female. Vertical axis shows her Cs, and horizontal axis shows the mean Cs of her preferred associates (as defined in *Materials and Methods*). This is plotted separately for preferred associates with high relatedness (circles) and preferred associates with low relatedness (squares). Relatedness cutoff values are defined in *Materials and Methods*. The relationship between females' Cs and mean Cs of their preferred associates changed depending on whether their preferred associates showed (*i*) high relatedness or (*ii*) low relatedness, as expected from Table 2, which showed significant interaction between social and genetic effects on Cs.

Materials and Methods

Study Site. The eastern gulf of Shark Bay is situated 850 km north of Perth in Western Australia (25°47′S, 113°43′E). The population of bottlenose dolphins (*Tursiops* sp.) has been the focus of extensive study since the mid-1980s (15, 38), making this study, along with the Sarasota, Florida, study (Wells et al., 14, 39, 40), one of the most comprehensive and detailed studies of bottlenose dolphins.

Calving Success and Age. We used life history data on 52 female bottlenose dolphins (*Tursiops* sp.) collected as a part of an ongoing longitudinal field study between 1984 and 2004. Female Cs was defined as the number of offspring surviving to age three divided by the number of years of reproductive data available for that particular female. In other words, Cs is the proportion of years in which the female produces a calf of age 3 y. Age 3 y was chosen because although most calves nurse beyond age 3 y, no nursing calves older than 3 y died before weaning, indicating that a calf surviving to age 3 y will usually reach juvenile (weaned) status and thus will have the potential to pass its mother's genes on to the next generation. If a female was of known age, her total reproductive years were counted from her 12th year (13). Otherwise, reproductive years were counted from her first known birth. Female age was determined by known birthdate (accurate ± 6 mo) or was estimated based on ventral speckling rates for females of known age compared with speckling of females of unknown age.

Relatedness Matrix. In comparison with the study by Frentiu et al. (19), which used 11 microsatellites containing a total of 44 alleles, the relatedness matrix used in our study was estimated using 12 microsatellite loci containing a total of 147 alleles. The microsatellite data used here were generated from previous studies (41, 42). They showed no linkage disequilibrium, null alleles, or departure from Hardy–Weinberg equilibrium (41). Furthermore, there was no need to partition the dataset to accommodate population structure because, within our study locality, population subdivision was minimized by high gene flow between areas (42). After trials on our data (41), we chose to generate the relatedness matrix using the Queller and Goodnight relatedness index, which ranges between −1 and 1 (20). This index was also used in the study by Frentiu et al. (19). The relatedness matrix among the 52 females was generated using the allele frequencies measured from 218 individuals. The mean relatedness estimate for the whole population was 0.005 with a SE of 0.0002 and a 95% confidence interval of 0.0004. The pairwise relatedness estimates among the 52 females ranged from −0.44 to 0.68.

Social Matrix. The association matrix was generated using group composition and behavioral data collected from 11,964 group encounter surveys. Surveys were completed for each individual or group that was encountered, and group composition was assessed using standard photo-identification methods (43). Unidentified individuals as well as ambiguous identifications were removed from the analyses (~10%). Variation in effort between years could also bias the data, which we addressed in two ways (30). First, association estimates between pairs of females were calculated using the half-weight index (HWI) (21), generated from SOCPROG 2.2 (44). The HWI is the most appropriate association index when members of each possible pair are more likely to be scored when separate than when together (21). The HWI ranges from 0 (never seen together) to 1 (never seen apart). Second, only females sighted more than 30 times were included in the analysis, so as to increase the likelihood to have sampled all possible associations and to ensure that females were sighted in multiple years. We also excluded nursing calves from the analysis due to their unique dependent relationship with their mothers (13).

Identification of Preferred Associates for Table 2 and Fig. 2. For each female, we measured her pairwise association estimates to all other females in the study as described above. Pairwise association estimates are nonnormally distributed. Therefore, a female's cutoff value for preferred associates was measured as any pairwise association estimates equal to or above that female's 97.5% percentile HWI distribution. We used such a conservative (i.e., high) cutoff value to increase the probability of capturing real preferred associations (most often seen with). Although we investigated other methodologies to categorize preferred associations, we found that the other methodologies were more appropriate for male alliances or did not account for individual variation in the degree of sociality (45).

Identification of Close Relatives for Table 2 and Fig. 2. For each female, we measured her pairwise relatedness estimates to all other females in the study as described above. Pairwise relatedness estimates are normally distributed. Therefore, a female's cutoff value for close relatives was calculated as any pairwise relatedness estimates two or more SDs above her mean relatedness to all other females (n = 51). At the other end of the relatedness spectrum, a female's cutoff value for distant relatives was calculated as any pairwise relatedness estimates two or more SDs below her mean relatedness to all other females (n = 51). We used such a conservative (i.e., high) cutoff value to increase the probability of capturing a female's closest relatives.

Home Range Size. As in the work by Frère et al. (30), home ranges (km^2) were measured using survey and focal follow data using the last sighting of each female per day. These points were restricted to well-surveyed areas, as determined by global positioning system (GPS) logs of boat tracks (a proxy for search effort). Total home range area was calculated using 100% minimum convex polygons (Universal Transverse Mercator projection 1983, zone 49S; ESRI, ArcGIS v. 9.3, Hawth's Tools extension).

Quantitative Genetic Analysis with the Pedigree-Free Animal Model. Additive genetic variance components (A-G_V) and BLUP estimates of genetic breeding values (G-EBV) for Cs were generated using the pedigree-free animal model (19) based on restricted maximum-likelihood (REML) (46). The pedigree-free animal model was run using the PROC MIXED procedure in SAS (2001; SAS Institute). For (A-G_V), this particular mixed model uses estimates of relatedness derived entirely from molecular markers to extract the additive genetic component (19). Because pairwise estimates need to be represented in a positive-definite matrix in the REML approach, we tested the relatedness matrix for positive-definiteness (i.e., positive eigenvalues of all eigenvectors) by measuring the eigenvalues of the square matrices in PopTools (CSIRO, Canberra, Australia) version 3.0.3 (47). Although the upper and lower relatedness estimates of the relatedness matrix are identical (e.g., i-j = j-i), the relatedness matrix was still found to be negative-definite. Only the last three eigenvalues of 52 were negative, indicating that the departure from positive-definite was only minor. In the case of identical by descent matrices generated from microsatellites, the negative-definite attribute of the matrix may be due to internal inconsistencies in relatedness estimates among multiple individuals generated by pairwise estimators. This is because the construction of the relatedness matrix is not based on a joint distribution for all individuals, but it is computed for two individuals at a time, marginalizing over the rest. Relatedness estimates measured in this way result in approximate marginal probabilities in the relatedness matrix instead of a joint distribution. The occurrence of negative-definite matrices is common in genetics (48–51). Genetic covariance matrices are well known for being non–negative-definite, as are identity-by-descent matrices (50, 51). Bending procedures (48, 49), are commonly used to correct non–negative-definiteness in genetic matrices (52), as they bend matrices until their lowest eigenvalues exceed a preset limit (e.g., zero to achieve non–negative-definiteness). To transform our negative-definite relatedness matrix into a positive-definite matrix, we used the Fortran Program (IBM Mathematical Formula Translating System, San Rose, CA) stepwise bending procedure, called Bendpdf (48). This was done by regressing the eigenvalues of the product of the negative-definite relatedness and positive-definite reference covariance matrix toward their mean (48). In our case, the bended relatedness matrix showed an extremely good correlation with the nonbended relatedness matrix (Mantel test: $r = 0.9999$, $P < 0.0001$). The prebending and postbending matrices for 20 of 52 individuals are shown in Tables S4 and S5, and show that the bending procedure retained relative values of the relatedness estimates, but altered them to be smaller relative to the diagonal elements (unity), the most common bending procedure. Finally, to account for variation in number of records per female, we weighted the model by the number of years for which each female was monitored. Age was added as a fixed effect. The genetic narrow-sense heritability (h^2_G) was estimated as the ratio of the additive genetic variance (A-G_V) to the total phenotypic variance (VP = A-G_V + A-G_R). To give the best presentation of the explanatory power of our data and to enable comparison with other studies, we also measured the coefficient of additive genetic variance (CV_A-G) (53), which scales the additive genetic variance by the mean (μ) of the trait (CV_A-G = $100 \times (\sqrt{\text{A-}G_V})/\mu$trait).

Quantitative Social Analysis with the Pedigree-Free Animal Model. We also needed to create measures of the social effects on fitness comparable to genetic measures. To do this, we noted that the covariance matrices which form the basis of mixed models such as the pedigree-free animal model do not necessarily have to be genetic. Thus, the genetic relatedness matrix can easily be substituted by an association matrix (HWI). By use of the pedigree-free animal model, we were able to generate estimates of additive social variance components (A-S_V) and social BLUP estimates (S-EBV) of female fitness (Cs). Unlike the relatedness matrix, the HWI association matrix was

positive-definite and did not require any bending. Analogous to genetic heritability, the social effect (h^2_S) was estimated as the ratio of the additive social variance (A-S_V) to the total phenotypic variance (VP). We also measured the coefficient of additive social variance (CV_A-*S*) as detailed above. Details about fixed effects and weights of the pedigree-free animal model are described above.

Significance of the Pedigree-Free Animal Models. The animal model in PROC MIXED does not provide error estimates for heritabilities. These could be derived from errors for the additive and residual variation, but only under assumptions that are unrealistic, such as normality and no covariance of additive and residual variation. Therefore, we chose to measure significance of the pedigree-free animal models using three different approaches. First, we used the null model likelihood ratio test in PROC MIXED. This "Null LRT" test measures significance by comparing the log-likelihood value of our full model (random + fixed effects) to log-likelihood value of a null model which only contains the fixed effects. PROC MIXED then measures $-2\times$ difference in log-likelihood between the full and null models. This test statistic, equal to twice the absolute difference in these log-likelihoods, is assumed to be distributed as χ^2 with 1 df. Second, in the "Const LRT" test, we tested whether the observed additive genetic and social variances were significantly different from zero. To do so, we compared the log-likelihood value of our full genetic and social models to the log-likelihood value of their relevant constrained models, in which the additive genetic and social covariances were set to zero using the parms function in SAS. We then measured $-2\times$ difference in log-likelihood between the unconstrained and constrained models, and assessed significance based on a χ^2 distribution with 1 df as described above. Last, we applied a randomization procedure ("Random") to assess whether the observed genetic heritability h^2_G and social h^2_S were greater than expected randomly. To do so, we generated random matrices by randomly allocating, with replacement, a female's pairwise estimates (social or relatedness) to each of the 51 females. We generated 100 such random relatedness and social matrices and measured their random additive genetic and social variances as well as their residuals. From these results, we assessed the number of times that random h^2_G and h^2_S estimates were found to be greater than or less than the observed estimates. Last, we investigated the robustness of our results by randomly removing one individual at a time from our dataset to test whether this would affect the significance of the h^2_G and h^2_S estimates.

GLMM. To investigate how genetic and social relationships might interact to affect the Cs, we analyzed the interactions between female Cs and (*i*) the mean Cs of their preferred associates, and (*ii*) the mean Cs of their close relatives, we fitted a GLMM. This allows one to deal with nonnormal data by using link functions and the exponential family (54). In our GLMM model, each female's Cs was treated as the response variable. To account for variation in the number of records per female, we weighted the model by the number of years for which each female was monitored. We incorporated female identity as a random factor to control for individual effects. Because Cs is a proportion, the error structure was fitted with a binomial distribution (54). In addition to the GLMM significance methodology, we also tested for significant departure from a null model using the Wald test. GLMMs and Wald tests were conducted using the lme4 package in R (R Development Core Team, Vienna).

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