Heritable victimization and the benefits of agonistic relationships

Amanda J. Lea[a], Daniel T. Blumstein[a,1], Tina W. Wey[a], and Julien G. A. Martin[b]

[a]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606; and [b]Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada J1K 2R1

Edited by James Hemphill Brown, University of New Mexico, Albuquerque, NM, and approved October 19, 2010 (received for review July 11, 2010)

Here, we present estimates of heritability and selection on network traits in a single population, allowing us to address the evolutionary potential of social behavior and the poorly understood link between sociality and fitness. To evolve, sociality must have some heritable basis, yet the heritability of social relationships is largely unknown. Recent advances in both social network analyses and quantitative genetics allow us to quantify attributes of social relationships and estimate their heritability in free-living populations. Our analyses addressed a variety of measures (in-degree, out-degree, attractiveness, expansiveness, embeddedness, and betweenness), and we hypothesized that traits reflecting relationships controlled by an individual (i.e., those that the individual initiated or were directly involved in) would be more heritable than those based largely on the behavior of conspecifics. Identifying patterns of heritability and selection among related traits may provide insight into which types of relationships are important in animal societies. As expected, we found that variation in indirect measures was largely explained by nongenetic variation. Yet, surprisingly, traits capturing initiated interactions do not possess significant additive genetic variation, whereas measures of received interactions are heritable. Measures describing initiated aggression and position in an agonistic network are under selection ($0.3 < |S| < 0.4$), although advantageous trait values are not inherited by offspring. It appears that agonistic relationships positively influence fitness and seemingly costly or harmful ties may, in fact, be beneficial. Our study highlights the importance of studying agonistic as well as affiliative relationships to understand fully the connections between sociality and fitness.

animal model | animal social networks | yellow-bellied marmots

Behavioral ecologists have long viewed sociality and social relationships as adaptive traits shaped by evolution (1, 2). However, if we are to study the evolution of sociality and social relationships, there must be heritable variation in traits describing individual social behavior. Numerous studies have identified heritable variation in animal dispositions (3, 4), morphological characteristics, and behavioral traits (5) that may affect how individuals interact with conspecifics, yet the role of genetics in social interactions themselves is poorly understood. If traits affecting social interactions are heritable, we may expect measures of social relationships to be explained somewhat by additive genetic factors.

There has been a recent upsurge in using animal social networks as tools for studying the ecology, evolution, and adaptive significance of sociality (6–8). Networks are based on interactions between individuals, and a variety of measures have been developed to quantify how connected individuals are with others in the group (9). Although studies of nonhuman species have explored the development of social networks (10) as well as the causes (11–13) and consequences (14–16) of network structure and individual position, no study has addressed the heritability of social network traits. If networks are to be useful tools for studying the evolution and maintenance of sociality, there must be heritable variation in network parameters.

To our knowledge, the only previous quantitative genetic study of social network traits was conducted in humans (17); that study reported sizeable heritabilities for the number of times an individual was named as a friend by others (in-degree, $h^2 = 0.46$), the likelihood that friends of the individual were connected to each other (transitivity or clustering coefficient, $h^2 = 0.47$), and the proportion of connections between individuals in the network that pass through the individual (betweenness, $h^2 = 0.29$), but it but found no evidence for additive genetic variation in how many friends a person named (out-degree). The authors proposed an attract and induce model of network formation in which additive genetic variation in initiated and received behaviors was required to generate heritabilities similar to real-life estimates. This approach refuted previous models of human social network formation based on a single interaction type, suggesting that networks cannot evolve from initiated or received interactions alone (18).

We wished to understand the genetic architecture of social relationships further as well as the poorly understood link between sociality and fitness (2), in a population of free-living nonhuman mammals. Furthermore, we wished to identify patterns among similar traits in an attempt to discover which interaction types are important in animal social networks. Previous studies of yellow-bellied marmot (*Marmota flaviventris*) social networks have addressed the robustness of network estimates (7), the correlations between network position and dispersal (15), and the roles of age and kinship in structuring networks (10); however, the genetic basis and fitness consequences of network traits are unknown.

We used social networks constructed from affiliative and agonistic interactions separately to estimate the heritability and fitness consequences of social network traits in marmots. Networks consisted of nodes (in this case, individual marmots) connected by binary links (i.e., 1/0 indicating the presence or absence of interactions between individuals). In our study, out-degree is the number of social partners toward which an individual initiates interactions, whereas in-degree represents the number of social partners from which an individual receives interactions. Expansiveness and attractiveness are similar to out-degree and in-degree but control for network density and reciprocity; these measures reflect an individual's tendency to initiate and receive interactions relative to the tendencies of other individuals in the network. We included two additional measures capturing more complex information about network position and integration: betweenness (reflecting an individual's importance as a connection point) and embeddedness (a measure of social cohesion) (19). These measures are partially based

Author contributions: D.T.B. designed research; A.J.L., D.T.B., and T.W.W. performed research; T.W.W. and J.G.A.M. analyzed data; and A.J.L., D.T.B., T.W.W., and J.G.A.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. E-mail: marmots@ucla.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1009882107/-/DCSupplemental.

on the relationships among an individual's connections, and such links are known as indirect interactions (7). We categorized network measures in terms of their directionality (initiated vs. received), type (direct vs. indirect), and nature (affiliative vs. agonistic) and predicted that similar traits would have similar selective pressures, and therefore comparable heritabilities and selection differentials. We hypothesized that social interactions controlled by an individual (i.e., those that are initiated or directly involve the focal animal) would be more heritable than those determined by the behavior of conspecifics, because such traits would be less determined by environmental variation. Although this line of thought [specifically hypothesis (*i*) as stated below] contradicts results from the previously discussed human network study, we believed that individual control would be important for explaining additive genetic variation in marmot social networks. We therefore predicted that (*i*) measures capturing an animal's tendency to initiate (i.e., out-degree, expansiveness) interactions are more heritable than those capturing an animal's tendency to receive (i.e., in-degree, attractiveness) interactions and (*ii*) measures based on direct interactions (i.e., out-degree, expansiveness, in-degree, attractiveness) are more heritable than those based on indirect (or a mixture of direct and indirect) interactions (i.e., betweenness, embeddedness).

We tested these hypotheses by estimating the heritabilities of six social network statistics based on affiliative and agonistic interactions (for a total of 12 measures, Table 1) to understand the role of each trait category in marmot networks. Furthermore, we quantified the magnitude of selection for all traits and examined correlations (genetic and phenotypic) that may explain behavioral patterns. Here, we decompose social behavior and address the heritability and fitness consequences of its individual parts.

Results

Contrary to our first hypothesis, network traits capturing initiated interactions did not possess significant additive genetic variation (Table 1), although three (agonistic in-degree and attractiveness, affiliative in-degree) of the four received measures were moderately ($h^2 < 0.2$) heritable. These heritable received measures represent a subset of the measures based on direct interactions (3 of 8). Although the majority of network traits describing direct interactions lack significant additive genetic variance, none of the measures describing indirect interactions were found to be heritable. In our study, social network measures based on direct interactions tend to be more heritable than those based on indirect interactions. Furthermore, variation in measures of indirect interactions is largely explained by permanent environment and social group, whereas these random factors play a less consistent role among measures of direct interactions (Fig. 1).

The majority of affiliative and agonistic network traits are phenotypically, although not genetically, correlated. Only agonistic in-degree and affiliative in-degree were genetically correlated [$r_G = 0.959 \pm 0.102$ SE, log-likelihood ratio test (LRT) = 3.86, $P = 0.049$]. There were significant phenotypic correlations between agonistic and affiliative out-degree ($r_P = 0.689 \pm 0.029$ SE, LRT = 16.43, $P < 0.001$), in-degree ($r_P = 0.570 \pm 0.040$ SE, LRT = 18.02, $P < 0.001$), betweenness ($r_P = 0.444 \pm 0.042$ SE, LRT = 7.36, $P = 0.001$), and embeddedness ($r_P = 0.648 \pm 0.033$ SE, LRT = 18.25, $P < 0.001$).

We found evidence of directional selection in the majority (8 of 12) of social network measures (Table 1). Stabilizing selection was less common (6 of 12) and was consistently lower in magnitude (all $|C| < 0.01$) than estimates of directional selection. Significant directional selection differentials for lifetime reproductive success (LRS) tended to be more common (LRS, 8 of 12; longevity, 3 of 12) and larger in magnitude (all $|S| > 0.19$) than those observed for longevity (all $|S| < 0.19$). Both initiated agonistic measures are under moderate selection ($|S| > 0.37$), although neither is heritable. Affiliative out-degree and in-degree are under some selection, although only in-degree is heritable, and consequently possesses some evolutionary potential. Individuals with high agonistic betweenness, agonistic embeddedness, and affiliative embeddedness have increased reproductive success (all $|S| > 0.30$); however, neither betweenness nor embeddedness is heritable in agonistic or affiliative networks.

Discussion

We hypothesized that social network measures capturing interactions controlled by an individual (direct and initiated) would be more heritable than measures based on indirect and received interactions. This rationale was confirmed in our second prediction (*ii*); measures of indirect interactions, which depend on the behavior of other group members, were not heritable. Interestingly, our first prediction (*i*) was strongly refuted; the majority of received (and both received agonistic) measures were heritable, whereas none of the initiated measures were explained by additive genetic variation. These results clearly refute the attract and induce model of human network formation (17), which requires additive genetic variation in measures of initiated and received interactions to explain real-life heritability estimates. Clearly, more studies addressing the quantitative genetics of social networks are needed to understand trends across species. In our study, patterns among agonistic traits may provide insight into the role of aggressive interactions in marmot societies.

Sociality should evolve when the benefits of group living (e.g., protection from predators, mating opportunities) exceed the costs [e.g., resource competition, exposure to disease (2, 20)]. However, group living inevitably leads to competition over limited resources (e.g., mates, habitat, food), and variation in aggressive behavior may therefore influence fitness (when more competitive individuals gain access to resources). Assuming that additive genetic variation is present, agonistic behavior should evolve and spread via natural selection. In yellow-bellied marmots, traits describing individual initiated agonistic relationships are not heritable. These traits are, however, under strong selection (longevity, $S > 0.15$; LRS, $S > 0.37$), and we expect such fitness-related traits to be rapidly fixed in the population (21). Thus, the lack of additive genetic variation in initiated aggression may suggest a crucial role for agonistic behavior in marmot societies. In fact, dominant individuals obtain increased access to high-quality burrows and foraging sites (22) as well as reproductive opportunities (23); furthermore, female marmots classified as aggressive produce more offspring than those classified as having a social or submissive-avoider behavioral phenotype (24). It appears that within-group competition is strong in marmot societies; initiated agonistic behavior therefore has profound fitness consequences, and additive genetic variation was likely depleted by past selection.

Interestingly, we found stronger overall selection on LRS than longevity for traits describing initiated agonistic interactions. Marmots initiating agonistic interactions with more social partners have increased longevity, but individual survival is largely unaffected by received agonistic interactions (as measured by in-degree and attractiveness) or affiliative relationships. These results may differ in more cooperative species or in those that form coalitions, because affiliative interactions may have a profound impact on survival in such societies. Future studies could address the fitness consequences (longevity vs. LRS) of social interactions in other types of animal societies to clarify this issue.

Although we may expect genetic variation in received aggression to influence fitness similarly and be depleted by selection, agonistic attractiveness ($h^2 = 0.177$) and in-degree ($h^2 = 0.112$) are heritable. Furthermore, individuals receiving more agonistic interactions (relative to others in the network) have decreased LRS ($S = -0.243$), and agonistic attractiveness may therefore evolve. Heritability in received aggression traits may be linked to additive genetic variation in dominance rank (25, 26) or

Table 1. Variance estimates and selection differentials for agonistic and affiliative social network measures

				Proportion of variance				LRS		Longevity	
Trait	Description	Mean (SD)	N_1	Additive genetic	Permanent environment	Social group	N_2	*S*	*C*	*S*	*C*
Agonistic											
Out-degree	Direct, initiated	2.030 (2.922)	367 (152)	0.017 (0.050)	**0.257 (0.074)**	0.078 (0.040)	256 (118)	**0.401 (0.082)**	−0.003 (0.001)	**0.159 (0.069)**	**−0.003 (0.001)**
In-degree	Direct, received	1.256 (1.393)	367 (152)	**0.112 (0.068)**	0.033 (0.061)	**0.161 (0.049)**	256 (118)	0.07 (0.066)	−0.003 (0.003)	−0.006 (0.054)	0 (0.002)
Expansiveness	Direct, initiated	0.253 (1.250)	214 (102)	0	0.100 (0.081)	0.033 (0.060)	136 (90)	**0.374 (0.091)**	−0.006 (0.006)	**0.189 (0.069)**	0.002 (0.005)
Attractiveness	Direct, received	−0.154 (0.815)	217 (107)	**0.177 (0.093)**	0	0	143 (92)	**−0.243 (0.07)**	**−0.019 (0.009)**	−0.039 (0.057)	−0.004 (0.007)
Betweenness	Indirect	3.133 (6.708)	367 (152)	0	**0.130 (0.053)**	0.019 (0.033)	256 (118)	**0.322 (0.075)**	−0.001 (0.001)	**0.177 (0.066)**	0 (0.001)
Embeddedness	Direct and indirect	1.711 (1.446)	367 (152)	0.066 (0.065)	**0.155 (0.070)**	**0.233 (0.057)**	256 (118)	**0.302 (0.079)**	−0.001 (0.002)	0.084 (0.063)	−0.004 (0.002)
Affiliative											
Out-degree	Direct, initiated	2.589 (2.830)	367 (152)	0.080 (0.070)	**0.240 (0.080)**	0.030 (0.030)	256 (118)	**0.263 (0.078)**	−0.002 (0.001)	0.039 (0.065)	−0.001 (0.001)
In-degree	Direct, received	2.447 (2.391)	367 (152)	**0.106 (0.065)**	0.085 (0.069)	0.054 (0.037)	256 (118)	**0.191 (0.07)**	**−0.005 (0.001)**	0.066 (0.055)	0 (0.001)
Expansiveness	Direct, initiated	−0.072 (1.263)	268 (120)	0	0.037 (0.058)	0.153 (0.073)	179 (102)	0.111 (0.073)	0 (0.005)	0.016 (0.063)	−0.003 (0.004)
Attractiveness	Direct, received	−0.185 (1.184)	268 (107)	0.078 (0.058)	0	0.067 (0.060)	170 (100)	−0.081 (0.079)	−0.001 (0.006)	−0.039 (0.062)	**0.009 (0.004)**
Betweenness	Indirect	2.301 (4.726)	367 (152)	0	**0.136 (0.054)**	**0.082 (0.039)**	256 (118)	**0.218 (0.073)**	**−0.002 (0.001)**	0.039 (0.062)	0 (0.001)
Embeddedness	Direct and indirect	2.371 (2.292)	367 (152)	0.087 (0.067)	**0.163 (0.074)**	**0.110 (0.046)**	256 (118)	−0.12 (0.064)	0.002 (0.002)	−0.006 (0.051)	**0.003 (0.001)**

Each network trait was classified as direct (measure based solely on interactions including the individual) or indirect (measure based on interactions of others, the individual's position in the network, or attributes of the total network) and as initiated or received. Univariate animal models were used to estimate the proportion of variation (±SD) attributed to additive genetic factors (h^2), permanent environment, and social group using a sample size of N_1 [total number of observations (number of unique individuals)]. Directional (*S*) and nonlinear (*C*) selection differentials were estimated in bivariate animal models of sample size N_2. Bivariate models included LRS and longevity as fitness proxies. All significant results ($P > 0.05$) are indicated in bold.

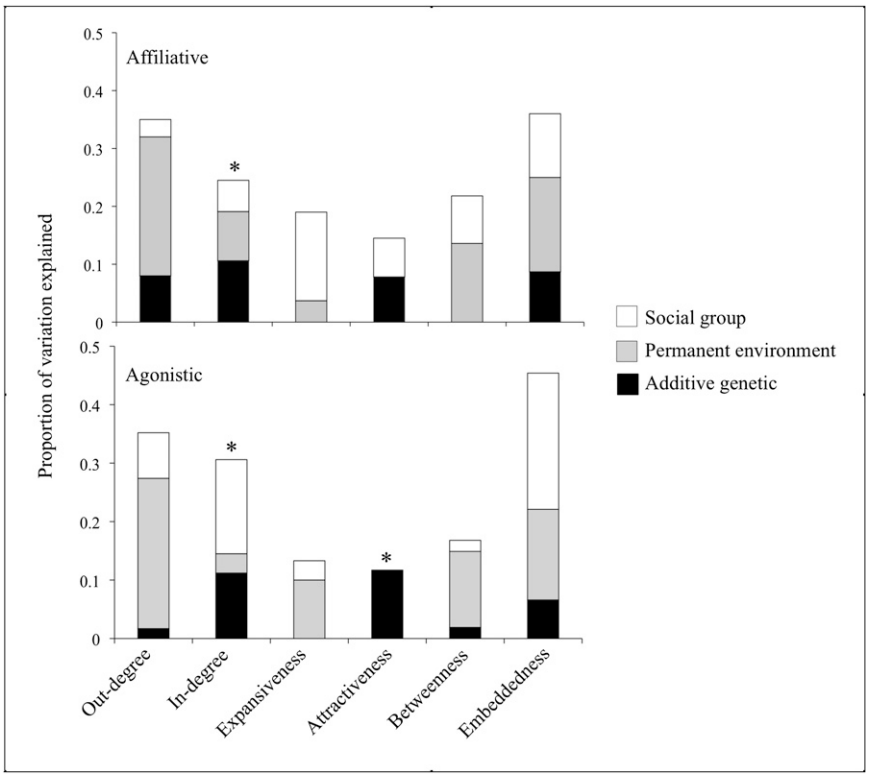

Fig. 1. Proportion of variation explained by social group, permanent environment, and additive genetic factors (h^2) for agonistic and affiliative social network measures. All estimates are from univariate animal models. Significant ($P < 0.05$) heritabilities are denoted by an asterisk.

personality (3, 4), with animals of low rank or certain dispositions easily victimized. We must also note the substantial ($R^2 = 0.959$) genetic correlation between agonistic and affiliative in-degree. The magnitude of this genetic correlation is surprising because we expect opposing selection pressures for agonistic and affiliative traits. However, we found no evidence for fitness consequences associated with agonistic in-degree, and change in this trait will likely result from directional selection on affiliative in-degree.

Although we report only one significant genetic correlation, we found a tendency for agonistic and affiliative network measures (specifically in-degree, out-degree, betweenness, and embeddedness) to be correlated at the phenotypic level. In other words, individuals involved in aggressive interactions with many individuals also socialize affiliatively with numerous conspecifics. Furthermore, marmots that are well connected and integrated in affiliative networks are also well connected and integrated in agonistic networks. Although affiliative and agonistic betweenness and embeddedness are not genetically correlated, certain individuals play more crucial roles in their group than others and this tendency is phenotypically expressed across network types.

In addition, we found embeddedness and betweenness (for both affiliative and agonistic networks) to covary with LRS and longevity, although these measures are not heritable and unlikely to evolve. It has long been assumed that, for social animals, interactions with conspecifics somehow influence reproductive success; however, the links between social relationships and fitness are still largely unresolved (2). In savanna baboons (*Papio cynocephalus*), infants of socially integrated female baboons (as measured by a composite index reflecting the proportion of time spent engaged in social behaviors) are more likely to survive (27), and it appears that social centrality and integration influence marmot fitness as well. Although anthropologists have long acknowledged an important role for social relationships in primates (28), rodents and nonprimate mammals have received less attention (cf. 29). Our results suggest that social integration and network position may have reproductive consequences in a wider range of species, including those with rudimentary sociality (30).

Furthermore, we present evidence for selection on social group position in agonistic networks. By constructing affiliative and agonistic networks separately, we were able to tease apart fitness consequences associated with each interaction type. This approach led us to a unique view of agonistic relationships, namely, that they are somehow beneficial. Previous studies linking social bonds and reproductive success have primarily focused on affiliative interactions (2), because such relationships have more immediate and obvious benefits [e.g., reduced stress (31, 32), enhanced immune competence (33)]. However, we found that the extent to which a marmot is integrated and centrally positioned in its agonistic network positively covaries with LRS and longevity. It is possible that a central and integrated position in the social group (which presumably results in more affiliative and agonistic partners and interactions) produces more benefits than the costs associated with the aggressive interactions themselves. Additionally, aggressive interactions in marmot societies may function to structure dominance hierarchies or maintain social order rather than seriously injuring or affecting recipients of aggressive interactions. We encourage future studies of adaptive social relationships to consider all interaction types, because seemingly costly or harmful ties may, in fact, benefit individual fitness.

Materials and Methods

Marmots were studied under research protocol ARC 2001-191-01 as well as permits issued by the Colorado Division of Wildlife. The research protocol was approved by the University of California Los Angeles Animal Care Committee on May 13, 2002, and was renewed annually. All subjects were members of a natural population living in and around the Rocky Mountain Biological Laboratory (RMBL; 38° 57′ North, 106° 59′ West), Gunnison County, CO. This population has been well studied since 1962 (34), and individuals remaining in the study area are live-trapped, individually marked (35), and closely monitored during their active season.

Marmots were observed several times a week over the 6-y period (total hours watched: 2003 = 698.48 h, 2004 = 783.76 h, 2005 = 775.04 h, 2006 = 847.21 h, 2007 = 1019.60 h, 2008 = 720.61 h) during times of peak activity (0700–1000 h and 1600–1900 h) from a distance that did not obviously affect the animals' behavior (20–150 m depending on habitat features). Social interactions between identified individuals were recorded using a detailed ethogram (15). Interactions were classified as affiliative (i.e., allogrooming, forage together within 1 m, greet, sit <1 m apart, play, sniff anogenital region) or agonistic (i.e., aggression, displacement) for analyses, with a small number of ambiguous interactions excluded from the dataset. Rare interactions between individuals who did not frequently associate were retained in the dataset. Although some studies of fission-fusion societies filter social relationships based on the number of observations (36), we believed rare interactions accurately reflected real relationships in marmot networks, which are geographically delimited and stable within a year. Eliminating weak relationships would potentially bias networks and discount the significance of infrequent social interactions.

Social networks were constructed in UCINET (37), and network measures were calculated using UCINET and the graphing software igraph (38) in the program R (version 2.10.1; R Development Core Team). We defined social networks as four geographically distinct colonies and determined yearly network membership from observations and trapping. Only individuals seen in the colony more than five times that year were included in network analysis (i.e., transient animals and their interactions were left out). Furthermore, we defined social networks annually because colony membership changes from year to year. Networks incorporated interactions between yearling and adult marmots; however, quantitative genetic analyses focused on adults (i.e., animals >2 y old), because the consistency of behavioral types is known to increase with age (39).

In total, network statistics were calculated for 24 social group-years over a 6-y period (2003–2008). Each social group represented a discrete network, and 12 measures were calculated for each member of the social group. Out-degree, in-degree, expansiveness, and attractiveness were based on directed networks (i.e., interactions have an initiator and recipient), whereas betweenness and embeddedness were calculated based on symmetrical networks (i.e., interactions are present or absent, with no directionality). Detailed information on these measures and how they are related to more traditional methods of quantifying social behavior (i.e., number and rate of interactions) is available in *SI Text* and elsewhere [degree and betweenness (9, 40, 41), expansiveness and attractiveness (42, 43), and embeddedness (15, 19)].

For all quantitative genetic analyses, we used a previously published (44) pedigree based on microsatellite genotypes and likelihood parentage assignment methods. We focused genetic analyses on a subset of individuals included in the pedigree for whom social network measures were available (sample sizes provided in Table 1). Heritabilities, genetic correlations, and fitness consequences were estimated using restricted maximum likelihood animal models (45, 46) in the program ASReml (47).

For each social network measure, we created separate univariate models, including fixed effects when significant, of social group size (for all traits except agonistic attractiveness, affiliative attractiveness, and affiliative expansiveness) and gender (for, agonistic out-degree expansiveness, and betweenness as well as affiliative out-degree, expansiveness, attractiveness, and betweenness); random effects were added to the model in an additive stepwise manner and evaluated with LRTs (df = 1). We examined random effects of permanent environment, maternal and paternal environment, paternal and maternal genetics, and social group (which accounts for year and location), with environmental effects retained in the model even when nonsignificant (48). Final models included random effects of social group, permanent environment, and individual identity (i.e., additive genetic) because these were found to explain significant variation in social network traits (Table 1). Because the phenotype of a given individual is invariably affected by other members of the network, social group was also retained as a random effect in all animal model analyses to control for nonindependence and the clustering of network measures. We estimated the proportion of variance explained by each random factor by dividing the variance from each random term by the total phenotypic variance (conditional on fixed effects). The identification and inclusion of fixed and random effects are therefore extremely important for accurately calculating heritability, because the estimate is dependent on the amount of additive genetic variance as well as variance explained by fixed effects (49). Heritability estimates are also especially vulnerable to the possibility that phenotypic similarities among relatives reflect shared environments rather than additive genetic variation (48). We have therefore tested and accounted for such common environment effects (i.e., social group, maternal and paternal environment) according to the method of Kruuk and Hadfield (48) and are confident that our heritability estimates truly represent genetic effects.

For each network statistic, we used bivariate models (with fixed and random effects from univariate models) to estimate the genetic and phenotypic covariance between agonistic and affiliative measures. The significance of each covariance estimate was assessed using the LRT, in which a model with the covariance term was compared with a model with the covariance term constrained to 0. Correlations were calculated by dividing the phenotypic [$COV_P(XY)$] and genetic [$COV_A(XY)$] covariances between the measured traits by the product of the single-trait SDs (V_{PX} and V_{PY}) for phenotypic and genetic variance [$r_P = COV_P(XY)/\sqrt{V_{PX}V_{PY}}$ and $r_A = COV_A(XY)/\sqrt{V_{PX}V_{PY}}$].

We used measures of LRS and longevity to assess the fitness consequences of each social network trait. LRS and longevity were calculated only for deceased individuals so as to avoid the problem of censored data. LRS was calculated directly from the pedigree, and longevity estimates were based on observation and trapping records; marmots at RMBL are extremely well trapped and observed, and individuals not sighted within a given year were therefore assumed to be dead (44).

We estimated linear (*S*) and nonlinear (*C*) standardized selection differentials for each measure using standard methods (50). *S* was estimated as the covariance between the measured trait and relative individual fitness. *C* was estimated as the covariance between relative individual fitness and the orthogonal quadratic estimate of the measured trait and represents the strength of stabilizing or disruptive selection independent of the effects of directional selection (50). Covariances were estimated in bivariate models, including the two fitness proxies as well as the measured trait (51). All bivariate models included a random effect of permanent environment as well as fixed effects from univariate models. Furthermore, both fitness proxies were corrected for gender to account for differential mortality and reproductive strategies among female and male marmots (52, 53). Covariance significance was assessed using the LRT statistic as described above.

ACKNOWLEDGMENTS. We thank our many marmoteers for collecting data over the years, especially Lucretia Olson for help with genetic analyses. We also thank Jennifer Smith, Ferenc Jordán, and two astute reviewers for comments on previous drafts. This work was supported by the University of California Los Angeles Academic Senate and Division of Life Sciences, The National Geographic Society, and the National Science Foundation (Grant NSF-IDBR-0754247 to D.T.B. and Grant DBI 0242960, 0731346 to the Rocky Mountain Biological Laboratory).

1. Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:25–38.
2. Silk JB (2007) The adaptive value of sociality in mammalian groups. *Philos Trans R Soc Lond B Biol Sci* 362:539–559.
3. Drent PJ, van Oers K, van Noordwijk AJ (2003) Realized heritability of personalities in the great tit (*Parus major*). *Proc Biol Sci* 270:45–51.
4. Sinn DL, Apiolaza LA, Moltschaniwskyj NA (2006) Heritability and fitness-related consequences of squid personality traits. *J Evol Biol* 19:1437–1447.
5. Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness components. *Heredity* 59:181–197.
6. Croft DP, James R, Krause J (2008) *Exploring Animal Social Networks* (Princeton Univ Press, Princeton).
7. Wey TW, Blumstein DT, Shen W, Jordon F (2008) Social network analysis of animal behaviour: A promising tool for the study of sociality. *Anim Behav* 75:333–344.
8. Sih A, Hanser SF, McHugh KA (2009) Social network theory: New insights and issues for behavioral ecologists. *Behav Ecol Sociobiol* 63:975–988.
9. Wasserman S, Faust K (1994) *Social Network Analysis: Methods and Applications* (Cambridge Univ Press, New York).
10. Wey TW, Blumstein DT (2010) Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim Behav* 79:1343–1352.
11. Lusseau D, Newman MEJ (2004) Identifying the role that animals play in their social networks. *Proc Biol Sci* 271(Suppl 6):S477–S481.
12. Pike TW, Samanta M, Lindström J, Royle NJ (2008) Behavioural phenotype affects social interactions in an animal network. *Proc Biol Sci* 275:2515–2520.
13. Madden JR, Drewe JA, Pearce GP, Clutton-Brock TH (2009) The social network structure of a wild meerkat population: 2. Intragroup interactions. *Behav Ecol Sociobiol* 64:81–95.
14. McDonald DB (2007) Predicting fate from early connectivity in a social network. *Proc Natl Acad Sci USA* 104:10910–10914.
15. Blumstein DT, Wey TW, Tang K (2009) A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proc Biol Sci* 276:3007–3012.
16. Voelkl B, Kasper C (2009) Social structure of primate interaction networks facilitates the emergence of cooperation. *Biol Lett* 5:462–464.
17. Fowler JH, Dawes CT, Christakis NA (2009) Model of genetic variation in human social networks. *Proc Natl Acad Sci USA* 106:1720–1724.

18. Jackson MO (2009) Genetic influences on social network characteristics. *Proc Natl Acad Sci USA* 106:1687–1688.
19. Moody J, White DR (2003) Social cohesion and embeddedness. *Am Sociol Rev* 68: 103–127.
20. Krause J, Ruxton GD (2002) *Living in Groups* (Oxford Univ Press, Oxford).
21. Kruuk LEB, et al. (2000) Heritability of fitness in a wild mammal population. *Proc Natl Acad Sci USA* 97:698–703.
22. Frase BA, Armitage KB (1984) Foraging patterns of yellow-bellied marmots: Role of kinship and individual variability. *Behav Ecol Sociobiol* 16:1–10.
23. Armitage KB (1986) Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology* 67:1186–1193.
24. Svendsen GE (1974) Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology* 55: 760–771.
25. Moore AJ (1990) The inheritance of social dominance, mating behavior and attractiveness to mates in male *Nauphoeta cinerea*. *Anim Behav* 39:388–397.
26. Nol E, Cheng K, Nichols C (1996) Heritability and phenotypic correlations of behaviour and dominance rank of Japanese quail. *Anim Behav* 52:813–820.
27. Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234.
28. Cheney DL, Seyfarth RM, Smuts B (1986) Social relationships and social cognition in nonhuman primates. *Science* 234:1361–1366.
29. Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. *Proc Natl Acad Sci USA* 106:13850–13853.
30. Olson LE, Blumstein DT (2010) Applying the coalitionary-traits metric: Sociality without cooperation in male yellow-bellied marmots. *Behav Ecol* 21:788–793.
31. Hennessy MB, Zate R, Maken DS (2008) Social buffering of the cortisol response of adult female guinea pigs. *Physiol Behav* 93:883–888.
32. Wittig RM, et al. (2008) Focused grooming networks and stress alleviation in wild female baboons. *Horm Behav* 54:170–177.
33. Kaplan JR, et al. (1991) The relationship of agonistic and affiliative behavior patterns to cellular-mediated immune function among cynomolgus monkeys (*Macaca fascicularis*) living in unstable social groups. *Am J Primatol* 25:157–173.
34. Ozgul A, et al. (2010) Phenotypic mechanisms underlying a demographic response to climate change. *Nature* 466:482–485.
35. Armitage KB (1982) *Yellow-Bellied Marmot* (CRC Press, Boca Raton, FL).
36. Rubenstein DI, Sundaresan S, Fischoff I, Saltz D (2007) *Exploration into the Biological Resources of Mongolia*, eds Stubbe A, Kaczensky P, Wesche K, Samjaa R, Stubbe M (Martin Luther University Halle-Wittenberg, Halle, Germany).
37. Borgatti SP, Everett MG, Freeman LC (2006) UCINET for Windows: Software for Social Network Analysis (Analytic Technologies, Harvard University, Cambridge, MA).
38. Csardi G, Nepusz T (2006) The igraph software package for complex social network research (InterJournal, Complex Systems p. 1695).
39. Barash D (1989) *Marmots: Social Behavior and Ecology* (Stanford Univ Press, Stanford, CA).
40. Freeman LC (1979) Centrality in social networks: Conceptual clarification. *Soc Networks* 1:215–239.
41. Friedkin NE (1991) Theoretical foundations for centrality measures. *Am J Sociol* 96: 1478–1504.
42. Skvoretz J, Faust K (1999) Logit models for affiliation networks. *Sociol Methodol* 29: 253–280.
43. Robins G, Pattison P, Kalish Y, Lusher D (2007) An introduction to exponential random graph (*p**) models for social networks. *Soc Networks* 29:173–191.
44. Blumstein DT, Lea AJ, Olson LE, Martin JGA (2010) Heritability of anti-predatory traits: Vigilance and locomotor performance in marmots. *J Evol Biol* 23:879–887.
45. Kruuk LEB (2004) Estimating genetic parameters in natural populations using the "animal model." *Philos Trans R Soc Lond B Biol Sci* 359:873–890.
46. Wilson AJ, et al. (2010) An ecologist's guide to the animal model. *J Anim Ecol* 79: 13–26.
47. Gilmour AR, Gogel BJ, Cullis BR, Thompson R (2004) *ASReml User Guide Release 2.0* (VSN International, Hemel Hempstead, United Kingdom).
48. Kruuk LEB, Hadfield JD (2007) How to separate genetic and environmental causes of similarity between relatives. *J Evol Biol* 20:1890–1903.
49. Wilson AJ (2008) Why h^2 does not always equal V A/V P? *J Evol Biol* 21:647–650.
50. Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
51. Hadfield JD (2008) Estimating evolutionary parameters when viability selection is operating. *Proc Biol Sci* 275:723–734.
52. Downhower JF, Armitage KB (1971) The yellow-bellied marmot and the evolution of polygamy. *Am Nat* 105:355–370.
53. Armitage KB (1998) Reproductive strategies of yellow-bellied marmots: Energy conservation and differences between the sexes. *J Mammal* 79:385–393.

Supporting Information

Lea et al. 10.1073/pnas.1009882107

SI Social Network Measures

Out-Degree and In-Degree. Degree in a nondirected (symmetrical) network (Fig. S1) is simply the number of other individuals in the network to which a focal individual is connected. Degree is one of the most basic concepts of individual importance in the network. It reflects only an individual's immediate interactions (i.e., only the "local" network), without controlling for any indirect interactions or overall network structure. An individual with higher degree (i.e., one that interacts with more individuals) is more interactive in a basic sense, is structurally more important, and can potentially influence more individuals through immediate connections.

In a directed network (i.e., when A → B is not the same as B → A; Fig. S2), degree is divided into out-degree and in-degree. In our marmot networks, out-degree is the number of other animals with which a focal animal initiates interactions, whereas in-degree is the number of other animals that direct interactions toward the focal animal. An animal with high out-degree may be relatively likely to influence other animals through initiated interactions, and an animal with high in-degree may be relatively likely to be influenced by other individuals through received interactions. We use out-degree and in-degree rather than simply degree because we predict that an animal's tendency to initiate or receive interactions may have fundamentally different mechanisms and consequences.

Betweenness. Betweenness is a measure of how important an individual is as a connection point between other individuals in the network. It is calculated as the proportion of shortest path lengths in the network on which the focal individual lies, where a path is the number of "social" steps connecting two individuals. For example, if A → B → C, there is a path of two steps between A and C, even if there is no immediate connection between A and C. Generally, an individual with high betweenness may have a high level of control over the flow of anything that may be transmitted (e.g., information, resources, disease) between other individuals in the network. In animal social networks, an animal with high betweenness may be important for maintaining social connections in the group and its removal may fragment the social group to a greater degree than the removal of an animal with lower betweenness. A fundamental concept in social network theory is that indirect interactions (i.e., connections of two or more social steps between individuals) are important, and unlike a measure such as degree, the calculation of betweenness incorporates both direct[†] and indirect interactions. Betweenness is most commonly calculated for symmetrical networks, and we use this version rather than a directed version of betweenness. We standardized betweenness for group size so that it was expressed as a proportion of the maximum possible value of betweenness in that network rather than as an absolute value to facilitate comparisons between groups of different sizes.

Expansiveness and Attractiveness. Expansiveness and attractiveness reflect an individual's tendency to initiate or receive interactions, respectively, relative to the tendencies of others in the social network. These measures thus capture similar concepts as out-degree and in-degree, but expansiveness and attractiveness are more sophisticated in the sense that they account for larger patterns of interaction in the overall network. The calculations of expansiveness and attractiveness use exponential random graph models or p^* models (1, 2), which model the probability of mutual, asymmetrical, or absent interactions in the network while controlling for overall network density (the number of interactions present relative to the number that could exist for a network of that size) and the overall reciprocity (tendency of interactions to be mutual: If A interacted with B, then B interacted with A). For each individual in the network, α- and β-parameters of relative initiation and reception are calculated, and we refer to these as expansiveness and attractiveness, respectively, as per some sociological literature (3). Expansiveness and attractiveness reflect an individual's importance in terms of its direct interactions but account for higher level patterns of interaction in the overall network. These two measures provide basic measures of a node's importance at a localized level (i.e., only to the extent of the node's immediate neighbors). Whereas out-degree and in-degree reflect an individual's level of interaction in an absolute sense, expansiveness and attractiveness reflect the individual's level of interaction in a relative sense.

Embeddedness. We use a measure of embeddedness that reflects social integration, as per Moody and White (4). In a network of nodes (individuals) and ties (interactions), a path is an alternating sequence of contiguous nodes and ties beginning and ending with the same node, in which no node occurs more than once. Paths are node-independent if they share no nodes. A k-component is a maximal subset of nodes in which all nodes are mutually reachable by at least k-node–independent paths using only nodes in the subset. Maximal means that no other node can be added to the set while ensuring that all members are still k-connected. A node's social embeddedness is the k of the largest k-component to which it belongs. As per Blumstein et al. (5), we extend the concept of social embeddedness as a biologically relevant measure of an animal's integration into a social group. For technical explanations of how embeddedness was calculated, we refer the reader to Fig. 1 and the *SI Text* of the article by Blumstein et al. (5); our analyses used similar methods.

Social Network Measures and Number/Rate of Interactions. Social network measures were calculated from raw data recording interactions between sets of individuals in a given social group. Social network measures capture more complex information about social relationships than simple measures of an individual's interaction frequency or rate, but results from the two approaches are related. We therefore investigated the relationship between the two approaches as well as the distribution of social interactions themselves. In Figs. S3–S6, we present frequency histograms summarizing the distribution of each social interaction type (Fig. S3, affiliative initiated; Fig. S4, agonistic received; Fig. S5, agonistic initiated; and Fig. S6, affiliative received) for individuals included in our dataset. Some individuals have few or no interactions recorded within a given year, but we do not believe this to be a sampling issue. Marmot social groups were extensively observed throughout the active season (800 h/y on average; exact number of hours watched per year is provided in *Materials and Methods*), but some individuals are not interactive [indeed, this species can be described as facultatively social (6)]. Nevertheless, our animal model analysis suggests that there is enough variability and within-individual

[†]Note the difference between "direct/indirect" and "directed/nondirected." Direct interactions occur between a pair of individuals. Indirect interactions between two individuals in the network occur through an intermediate individual. In nondirected or symmetrical networks, a connection between A – B is equivalent to B – A, whereas A → B is not the same as B → A in a directed network.

stability among network statistics to estimate significant individual differences; otherwise, significant additive genetic variation would not be possible.

To understand the relationship between annual individual interaction rate (number of interactions per hour watched for a given social group per year) and social network statistics, we used bivariate linear mixed effects models. Variation in each social network measure was explained by the appropriate interaction rate (i.e., affiliative initiated, affiliative received, agonistic initiated, agonistic received; Table S1). Individual identity, year, and social group were fitted as random effects. Phenotypic covariance was estimated as the sum of residual, year, social group, and identity covariance. Individual level correlation was estimated as covariance associated with individual identity divided by the square root of the product of variance associated with individual identity for each trait. Significance of individual level correlation was assessed using a LRT between models with and without individual level covariance effect. Furthermore, we estimated the heritability of interaction rates using an animal model, including year, social group, permanent environment, and additive genetic as random effects (details of model fitting are presented in *Materials and Methods*), to understand differences in additive genetic variance among our measures.

As expected, some network statistics are more related to interaction rates than others (Table S1); not surprisingly, in-degree and out-degree (which capture more basic features of relationships and interactions) are more highly related to rate than network statistics capturing complex information about network integration and position. For both agonistic and affiliative interactions, we found that rates of initiated interactions were not heritable (agonistic: $h^2 = 0.001 \pm 0.001$ SE, LRT < 0.001, $P = 0.99$; affiliative: $h^2 = 0.103 \pm 0.099$, LRT $= 1.652$, $P = 0.196$) whereas received rates were (agonistic: $h^2 = 0.179 \pm 0.064$, LRT $= 13.6$, $P < 0.001$; affiliative: $h^2 = 0.146 \pm 0.055$, LRT $= 11.56$, $P < 0.001$). These results parallel patterns of heritability observed for social network measures (i.e., measures based on received interactions were heritable, whereas those reflecting initiated interactions were not). Although a few results from an interaction rate analysis are similar to a network-based approach, much information is lost by using more traditional measures. Ultimately, we view network statistics as precisely describing individual attributes of sociality and providing a more comprehensive profile of individual relationships.

1. Faust K, Skvoretz J (2002) *Sociological Methodology*, ed Stolzenberg R (Blackwell Publishing, Cambridge, MA).
2. Robins G, Pattison P, Kalish Y, Lusher D (2007) An introduction to exponential random graph (*p**) models for social networks. *Soc Networks* 29:173–191.
3. Skvoretz J, Faust K (1999) Logit models for affiliation networks. *Sociol Methodol* 29: 253–280.
4. Moody J, White DR (2003) Social cohesion and embeddedness. *Am Sociol Rev* 68: 103–127.
5. Blumstein DT, Wey TW, Tang K (2009) A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proc Biol Sci* 276:3007–3012.
6. Blumstein DT, Armitage KB (1999) Cooperative breeding in marmots. *Oikos* 84: 369–382.

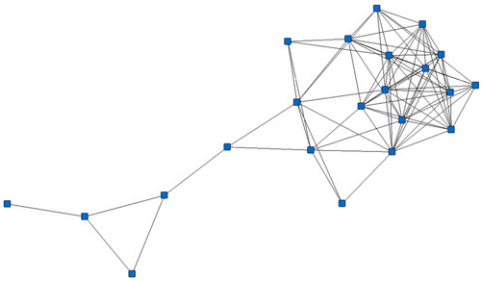

Fig. S1. Example of a nondirected (symmetrical) marmot social network based on affiliative interactions.

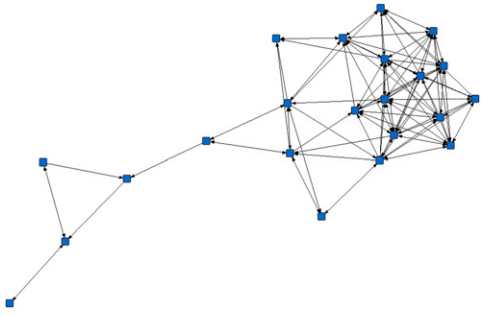

Fig. S2. Example of a directed marmot social network based on affiliative interactions, with arrows indicating the directionality of relationships. For example, an arrow terminating at a node (i.e., individual) indicates that the given individual received affiliative interactions from the individual at the arrow's origin.

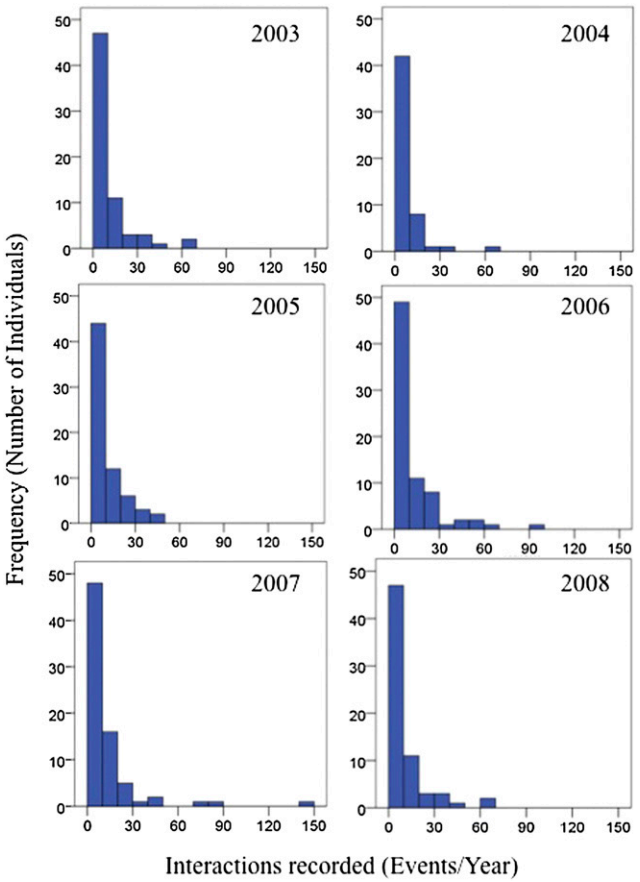

Fig. S3. Histograms displaying the number of affiliative initiated interactions recorded per individual from 2003 to 2008. Sample sizes are as follows: 2003, n = 30; 2004, n = 53; 2005, n = 67; 2006, n = 75; 2007, n = 75; and 2008, n = 67.

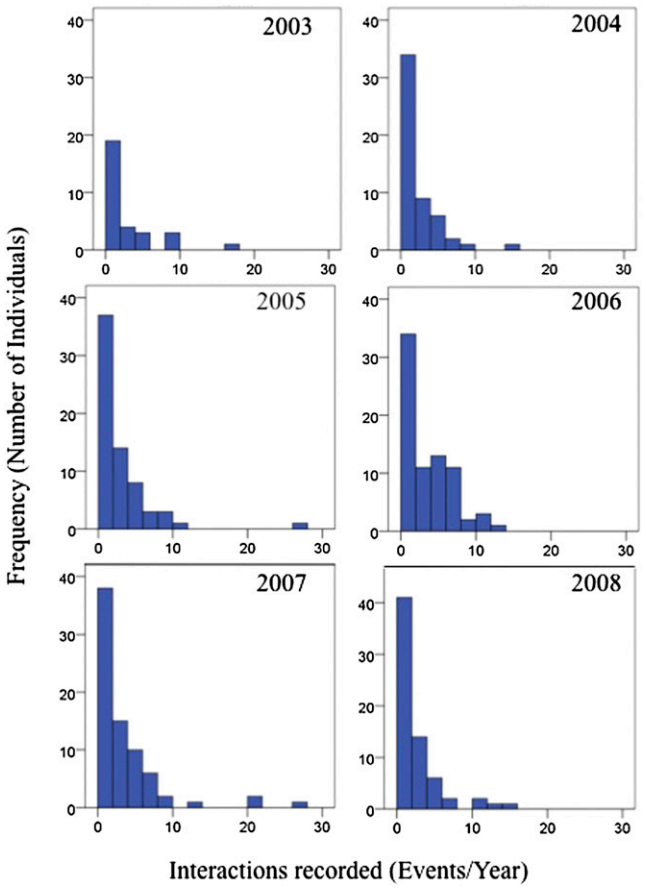

Fig. S4. Histograms displaying the number of agonistic received interactions recorded per individual from 2003 to 2008. Sample sizes are as follows: 2003, *n* = 30; 2004, *n* = 53; 2005, *n* = 67; 2006, *n* = 75; 2007, *n* = 75; and 2008, *n* = 67.

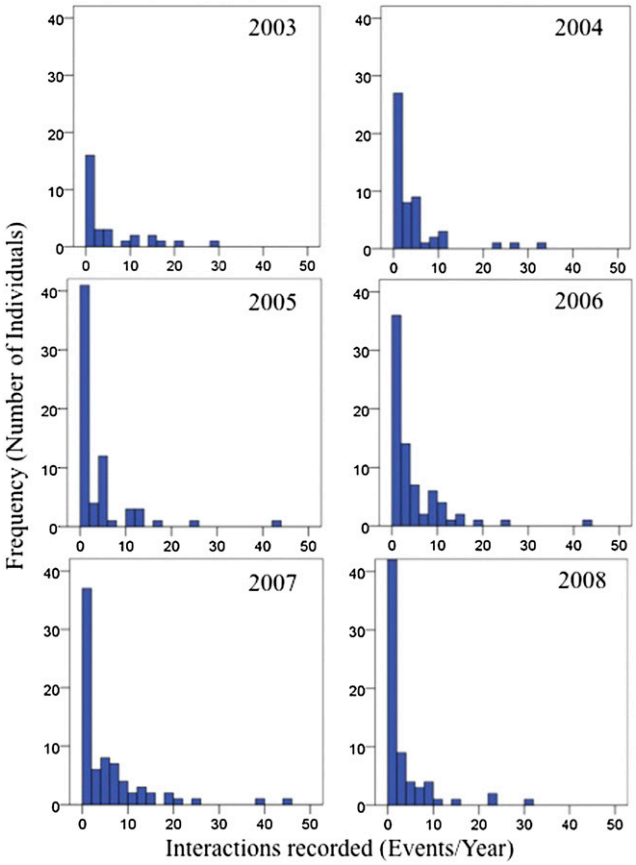

Fig. S5. Histograms displaying the number of agonistic initiated interactions recorded per individual from 2003 to 2008. Sample sizes are as follows: 2003, *n* = 30; 2004, *n* = 53; 2005, *n* = 67; 2006, *n* = 75; 2007, *n* = 75; and 2008, *n* = 67.

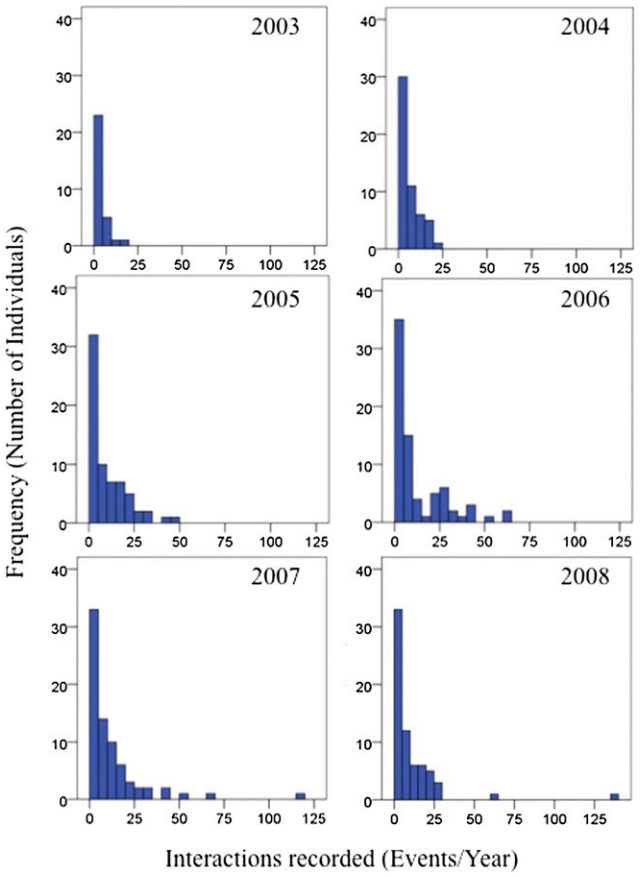

Fig. S6. Histograms displaying the number of affiliative received interactions recorded per individual from 2003 to 2008. Sample sizes are as follows: 2003, *n* = 30; 2004, *n* = 53; 2005, *n* = 67; 2006, *n* = 75; 2007, *n* = 75; and 2008, *n* = 67.

Table S1. Summary of relationships between interaction rate measures and social network statistics

Social network type	Interaction rate measure	Social network statistic	*N*	Phenotypic correlation	Individual level correlation	LRT	*P*
Agonistic	Initiated	Out-degree	152	0.850 (0.020)	0.964 (0.028)	29.152	<0.001
	Received	In-degree	152	0.723 (0.043)	1.035 (0.056)	13.140	<0.001
	Initiated	Expansiveness	102	0.548 (0.050)	0.981 (0.142)	15.116	<0.001
	Received	Attractiveness	107	0.277 (0.071)	0.172 (0.469)	0.020	0.888
	Initiated	Betweenness	152	0.549 (0.043)	0.861 (0.089)	19.550	<0.001
	Received	Betweenness	152	0.216 (0.062)	0.283 (0.227)	1.058	0.304
	Initiated	Embeddedness	152	0.562 (0.055)	0.958 (0.090)	22.570	<0.001
	Received	Embeddedness	152	0.518 (0.062)	1.022 (0.106)	20.146	<0.001
Affiliative	Initiated	Out-degree	152	0.650 (0.043)	1.132 (0.076)	30.940	<0.001
	Received	In-degree	152	0.527 (0.049)	0.964 (0.171)	9.832	0.002
	Initiated	Expansiveness	120	0.353 (0.055)	1.504 (0.290)	23.890	<0.001
	Received	Attractiveness	107	0.250 (0.054)	0.547 (0.386)	1.068	0.301
	Initiated	Betweenness	152	0.416 (0.052)	0.815 (0.130)	15.320	<0.001
	Received	Betweenness	152	0.301 (0.054)	0.567 (0.264)	2.779	0.096
	Initiated	Embeddedness	152	0.534 (0.060)	0.839 (0.093)	21.778	<0.001
	Received	Embeddedness	152	0.398 (0.062)	1.001 (0.211)	13.590	<0.001

Correlations were estimated using bivariate mixed models, including year, social group, and individual identity as random effects. *N* refers to the number of unique individuals included in each model.