Strong social relationships are associated with decreased longevity in a facultatively social mammal

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Abstract

Humans in strong social relationships are more likely to live longer because social relationships may buffer stressors and thus have protective effects. However, a shortcoming of human studies is that they often rely on self-reporting of these relationships. By contrast, observational studies of nonhuman animals permit detailed analyses of the specific nature of social relationships. Thus, discoveries that some social animals live longer and healthier lives if they are involved in social grooming, forage together, or have more affiliative associates emphasizes the potential importance of social relationships on health and longevity. Previous studies have focused on the impact of social metrics on longevity in obligately social species. However, if sociality indeed has a key role in longevity, we might expect that affiliative relationships should also influence longevity in less social species. We focused on socially flexible yellow-bellied marmots (*Marmota flaviventer*) and asked whether female longevity covaries with the specific nature of social relationships. We quantified social relationships with social network statistics that were based on affiliative interactions, and then estimated the correlation between longevity and sociality using bivariate models. We found a significant negative phenotypic correlation between affiliative social relationship strength and longevity; marmots with greater degree, closeness, and those with a greater negative average shortest path length died at younger ages. We conclude that sociality plays an important role in longevity, but how it does so may depend on whether a species is obligately or facultatively social.

Keywords: Social networks, health, longevity, social behaviour, yellow-bellied marmots

Introduction

Affiliative social relationships affect longevity in human and nonhuman animals through a variety of mechanisms [1, 2]. Strong affiliative social relationships enhance health and survival outcomes [3], but socially acquired pathogens [4] and social stressors [5] may reduce longevity. There are two main hypotheses that explain how strong affiliative relationships enhance longevity. The ‘buffering hypothesis’ suggests that the presence of an active social support system, that provides emotional, informational or tangible aid to the focal individual, creates a buffer against acute or chronic stressors, such as illness and stressful life events [6]. The ‘main effects’ hypothesis proposes that social relationships provide direct emotional and behavioural aid that was not necessarily intended as support, but may encourage lifestyle changes such as healthy behaviours [6]. For example, the ‘main effects’ hypothesis is at work when people conform to social norms relevant to self-care due to the presence of these behaviours in their social network [6]. In addition, particularly in humans, complex social relationships that influence an individual’s mental and physical health affect longevity through mechanisms such as social influence, sense of control, social control, role-based purpose and meaning, self-esteem, belonging and companionship, and perceived support availability [7]. A meta-analysis of 308,849 individuals across 148 studies revealed that humans with relatively strong social relationships increased their likelihood of survival by 50% [6]. Thus, improving human longevity requires an appropriate understanding of the specific ways in which social interactions influence longevity [5,8]. For instance, social interactions can be direct, and involve specific relationships with others or be more indirect and involve an individual’s position in a more complex social network.

An important shortcoming of human studies is that they are often limited to self-reports and interviews. Self-reporting is conflated by biases, including social desirability bias, recall bias, and confirmation bias [9]. These methods are also unable to identify the specific type of social relationship that may enhance health and longevity. By comparison, studies of individually marked animals permit researchers to directly observe and score social interactions, which permits detailed, objective analyses of the specific nature of social relationships.

Studies of longevity in nonhumans have identified a number of ways in which sociality influences health and longevity. Using a 'composite sociality index' (CSI) to characterize affiliative relationships within dyads, it was shown that female chacma baboons (*Papio hamadryas ursinas*) who formed stronger and more stable social bonds with other females lived significantly longer than females who were in weaker and less stable relationships [10]. Similarly, female macaques with a higher degree in their social networks (i.e. they interacted more with conspecifics) or who had more relatives had higher survival [11]. In bighorn sheep (*Ovis canadensis),* which have fission-fusion social groups, female centrality (a measure of the degree to which individuals were well-connected with others in their group) has a positive effect on lamb production and fitness [12]. Other affiliative social network metrics also capture the effects of direct and indirect social relationships on health and longevity. For example, adult longevity in rock hyraxes (*Procavia capensis*) was inversely correlated with the variation in a group's centrality [13]; hyraxes in groups with relatively more equal associations lived longer. Juvenile male bottlenose dolphins (*Tursiops* sp.) with higher eigenvector centrality, which takes into account indirect social relationships, had higher survival [14]. These results seem to suggest that in obligately social animals, longevity is enhanced in individuals with more associates, stronger bonds, and in those who were more connected with others in their group [15].

If sociality, or the two main hypotheses explaining it ('buffering' and 'main effects' hypotheses), has a key role in affecting longevity, we might expect that affiliative relationships would also influence longevity in less social or facultatively social species. By facultatively social, we mean that individuals have some degree of social flexibility and may be found in different size groups where they may or may not cooperate with others. We focused on facultatively social yellow-bellied marmots (*Marmota flaviventer*) and asked whether female longevity covaries with the strength of their social relationships. Marmots at our site have been studied since 1962 [16,17] and prior results have shown that they are often harem polygynous [17]. However, yellow-bellied marmots also live in a variety of group sizes, ranging from solitary females to females living with a single male, their young of the year and some yearlings, to females living in multi-female groups, with young and pre-dispersal yearlings from different females [17]. This social flexibility provides a unique opportunity to study the consequences of social variation [16]. They are also an excellent species in which to study the relationship between sociality and longevity because they are diurnal and can be easily located, trapped, marked, and observed throughout their lives. Regular trapping and observations throughout the 5-6 month active season permits births and deaths of residents to be known with certainty. In addition, social relationships are not only heritable [18], but also have important ecological consequences [16,19,20].

We capitalised on marmot social flexibility to study the covariation between a suite of specific social network measures, which measure the quantity and strength of social relationships, and longevity. Both the ‘buffering’ and the ‘main effects’ hypotheses predict enhanced longevity for individuals with relatively more affiliative interactions. We thus hypothesise that marmots with higher social network trait values in affiliative interaction networks will live longer.

Materials and methods

Study site and subjects

Between 2002 and 2015, we studied yellow-bellied marmots located in the upper East River Valley in and around the Rocky Mountain Biological Laboratory, Gothic, Colorado (38°57' N, 106°59' W). We studied marmots along a 5 km section of a single valley that is subdivided into lower and higher elevation sections [17]. Marmots live in colonies and each colony contains one or more social groups, which are defined based on space-use overlap and burrow sharing [19, 21]. Marmot colony sites vary in their suitability and some sites have been consistently occupied for the past 55 years, while others periodically go extinct [22, 23]. We examined 11 colonies that have been studied consistently since 2002, creating a data set of 79 colony years (a colony studied for a year). During our study, these colonies ranged in size from 1 to 24 individuals (X±SD = 6.4±4.9).

Marmots were trapped on a bi-weekly basis every summer and individually marked for identification. All individuals trapped for the first time as juveniles or yearlings were thus of known age. Mortality was inferred for individuals not seen in consecutive years. Capture-Mark-Recapture analysis shows that >98% of living individuals are captured annually [24], and thus longevity estimates for individuals of known age were accurate. Maximum female longevity at our study site is 16 years [23]. Overwinter mortality and predation during the active season are the main sources of adult resident mortality [17] and when an otherwise healthy adult female suddenly disappears during the summer, we infer predation.

Stress hormone levels have previously been known to influence longevity via a variety of mechanisms [25]. We use faecal glucocorticoid metabolites as a measure of stress in marmots. Fecal samples were collected, when available, during capture events. Faecal samples were stored on ice and later frozen at -20°C. Faecal glucocorticoid metabolites were extracted and quantified at the end of each year using established protocols [26] and a validated assay [27].

Social measures

Social interactions were recorded during near daily observations when it was not snowing or raining by observers quietly seated 20-150 m away using binoculars and 15-45x spotting scopes. Multiple observers recorded data in a given year and, before recording data, each observer was trained to identify subjects using their unique fur marks, and trained with our marmot social ethogram and videos of marmot interactions to consistently score social interactions. Individuals typically interact with members of the same group and observers recorded all social interactions between marmots that they could detect using all occurrence sampling [22]. Since social interactions are rare and obvious, they are missed using focal animal sampling; thus, all occurrence sampling is more appropriate in this system. In addition, because social interactions are rare, we included all interactions we could see. Thus, an individual could greet and then sit next to a conspecific and this would be scored as two unique social interactions. We also recognise that difficulties in detectability (because of vegetation and terrain) impact our ability to quantify all observations, but we have no way to correct for this. Observations occurred during hours of peak activity (7 - 10 h in the morning and 16 – 19 h in the afternoon from mid-April to mid-September [22].

Since yellow-bellied marmots are matrilineal [17], we focused our study on female social relationships and removed both yearling males and adult males from all networks. There are no strong predictions about which specific measures of social relationship strength should be associated with longevity, so we created association matrices from a total of 5,639 affiliative interactions among 247 female yearlings and female adults at 11 geographically distinct colony sites and created female only weighted social networks, which take into account the number of repetitive interactions that occurred between two individuals. We then calculated a variety of social network metrics that describe how connected individuals are, either directly or indirectly, with others in their social group. We focused on affiliative interactions [28, 29] that included cohesive behaviors such as allogrooming, greeting, foraging together, playing together, and sitting in close proximity [19].

To estimate an individual's sociality, we calculated 11 social network statistics (indegree, outdegree, incloseness, outcloseness, local clustering, global clustering, betweenness centrality, eigenvector centrality, average shortest path, instrength and outstrength) from the weighted social networks using the package iGraph v. 1.0.1 [30] in R 3.2.3 [31]. The final social networks we analysed were constructed from an average of 13.3 observations (SD = 18.2). Larger social groups were characterised by significantly more social observations ($r = 0.92$, $p < 0.001$).

Indegree describes the number of individuals a focal individual receives interactions from, whereas outdegree describes the number of individuals with whom a focal individual initiates interactions [32]. Closeness describes how influential a focal individual is by measuring how close (i.e. through direct or indirect relationships) they are to all other individuals in the network, defined as the reciprocal of the sum of the shortest path lengths between a focal individual and all other network individuals [31]. Incloseness and outcloseness describe received and initiated interactions respectively. Clustering determines cliquishness of the network and is calculated by dividing the number of actual relationships formed between the focal individual and its' neighbors by the total possible number of relationships that could be formed by the focal individual [33]. Local clustering describes the embeddedness of a focal individual and global clustering indicates the density of the network around a focal individual [34, 32]. Betweenness centrality describes the proportion of shortest path lengths in the network between all other pairs of individuals connected to a focal individual [33]. Eigenvector centrality describes an individual's connectedness and takes into account the indirect relationships that occur between an individual's neighbors [35]. Average shortest path describes the efficiency of a network in transferring information and is calculated from the average number of individuals that a focal individual must go through in order to contact another member of its social network [35]. Strength describes the sum of the weights (frequency) of interactions between a focal individual and their adjacent neighbors [32, 34]. Instrength and outstrength describe received and initiated interactions respectively.

For all estimated social network attributes, except average shortest path, a larger value is interpreted as being more social. Conversely, for average shortest path, a larger value is interpreted as being less social. Thus, to facilitate the interpretation, we used the opposite of average shortest path which we refer to as "negative average shortest path". Thus, following our hypothesis, we expect positive correlations between all social network traits and longevity.

Statistical analyses

To test the influence of sociality on longevity, we fitted bivariate models of weighted social network metrics and longevity. To avoid selective disappearance biases, we restricted our analysis to extinct cohorts only. The final data set included 386 estimates for each of the 11 affiliative social network attributes for 76 unique individuals (some traits could not be calculated for each individual). Each bivariate model fitted a social network trait and log-transformed longevity as dependent variables. To facilitate model convergence and allow for comparison across traits, all variables were scaled with a mean of zero and a variance of one. For social network traits, valley, age and log-transformed faecal glucocorticoid metabolite level were fitted as fixed effects to correct for environmental, ageing and stress effects on sociality. Year was fitted as a random effect to account for annual variation in population structure. For longevity, valley was included as a fixed effect, and year of birth was fitted as a random effect to account for cohort effects. We fitted individual identity as a random effect for both traits. Since each individual has only one observation for longevity, we fixed the longevity residual variance and the residual covariance at 0, allowing us to estimate the covariation between longevity and social network traits at the individual level.

Models were fitted using a Bayesian approach using MCMCglmm [36] in R 3.2.3 [31]. We used flat priors at the correlation level for individual identity effect (i.e. parameter expanded prior: V = diag(2), nu = 3, alpha.mu = rep(0,2), alpha.V=diag(25^2,2)). Priors for cohort and year random effects were uninformative (V=1 and nu=0.002). The prior for the residual variance was uninformative for social traits and fixed at 0 for longevity (V = diag(1, 0.00002), nu = 1.002, fix = 2). Each bivariate model was run for 2,300,000 iterations with a thinning of 2,000 and a burning period of 300,000 iterations, which, for all parameters, produced autocorrelation coefficients < 0.1 and effective samples size between 910 and 1000.

Results

Some, but not all, of our fixed effects were significant; we focus first on network traits, and then on longevity. No variation in social traits was explained by FGM (Table 1), a finding that suggests no relation between stress and sociality. Age was significantly related only with eigenvector centrality (Table 1). Eigenvector centrality decreased with age suggesting that older females were less social; a finding previously reported [38]. Valley was significant only for global clustering, with individuals up-valley having higher clustering (Table 1). There was no effect of valley on longevity (Table S3).

All social network traits were repeatable with a non-zero between-individual variance (Table 2), and between-individual variance in longevity was similar across all models (Table 2). Out of 11 correlations between social traits and longevity, 9 were negative, 5 of them were significantly so, and one more (betweenness) cannot be said to be significantly different from zero, but is still negative since 96.5% of its posterior distribution was negative (Table 2 and Fig. 1). The two positive correlations were small and not significantly different from zero (Table 2). This was in stark contrast to our expectations that social attributes would generally be positively correlated with longevity. Marmots who were closer to others within their network, defined by greater in- and out-degree, in- and out-closeness, and negative average shortest path length, lived shorter lives (Table 2, Fig. 1). Results were similar (betweenness became significantly negative) when analyses were conducted on un-weighted social network measures (Supplementary Table S1).

Discussion

Previous studies in humans [37] and other obligately social mammals (e.g. [11,12]) identified significant positive correlations between individuals being in strong, affiliative social relationships and longevity. In yellow-bellied marmots, a facultatively social mammal, this pattern does not hold. We used formal social network measures of relationship strength, a relatively large sample size of long-lived free-living mammals, and the appropriate bivariate model that permitted us to isolate and estimate the covariance between sociality and longevity. We found that five of the eleven affiliative social network traits we measured were significantly associated with reduced lifespans. Stated succinctly, more social animals lived shorter lives. These results are inconsistent with what has been previously reported in humans and other species (see introduction) and do not support either the buffering or main effects hypotheses, which state that increased sociality should correlate with increasing longevity. Thus, these marmot results suggest that, in some species, strong social relationships need not be beneficial and may even be costly. In retrospect, the results may have been anticipated by a recent finding that yellow-bellied marmots with stronger affiliative relationships were more likely to die over-winter [20]. While that result focused solely on over-winter survival, the current study focused on overall longevity—which is influenced by both summer survival and over-winter survival. Thus, the current study was more comprehensive and explored the influence of more social network traits.

However, these somewhat paradoxical results are consistent with a suite of other findings from our population of yellow-bellied marmots. Female marmots in stronger affiliative relationships have reduced annual reproductive success [19], and marmots with stronger affiliative relationships during the summer are less likely to survive the following winter [20]. Older females become less social with age [38], and homophily rules that describe interactions based on age, sex and relatedness, seem to break down at larger group sizes [39]. Finally, there is significant heritable variation in the propensity to tolerate agonistic behaviour, but no significant heritable variation in the propensity to engage in affiliative behaviour [40]. Thus, while marmots are social, they are not necessarily cooperative [16] and they may not necessarily benefit from strong social relationships.

When population size increases and animals fail to disperse, marmots have the potential to interact with more individuals. However, individuals in larger groups do not necessarily benefit from increased social connectivity. In situations where dispersing animals leave a site with a relatively high probability of survival to go off to an uncertain fate, increased social connectivity may be adaptive for individuals that are otherwise likely to disperse because it strengthens relationships and reduces the likelihood of dispersal. Nevertheless, for established residents, increased social connectivity may be costly. This should be expected in situations where insider-outsider conflicts exist [41, 42]. In such situations, residents pay a cost when outsiders join groups, while outsiders join groups because they obtain greater fitness living socially compared to that when living alone.

Given our findings that social relationships are significantly negatively correlated with longevity in a facultatively social species, variation in social relationships may have profoundly different effects on population demography in highly social (e.g. obligately social species) and less social species (e.g. facultatively social and asocial species). Our results also suggest that both direct affiliative social relationships (degree and strength) as well as less direct affiliative relationships (betweeness centrality) may affect longevity. Additionally, the significance of both in- and out-degree suggests that it is not only affiliative actions that individuals initiated that negatively influence longevity, but also affiliative actions that they received and have little control over. Our findings prompt future questions about why affiliative interactions in particular have negative effects on individual survival.

Our results are inconsistent with both the buffering and main effects hypotheses; affiliative social interactions decreased longevity, suggesting that affiliative interaction does not act as a buffer to stress in the same ways that it does in other animals. We nevertheless illustrated the seminal importance of sociality effects on longevity. Additional studies on other facultatively social species may reveal whether this negative phenotypic correlation between sociality and longevity is typical of facultative sociality and would answer the question of whether being 'too social' may be costly in some species. Additionally, studies of systems characterized by insider-outsider dynamics that are created when animals disperse and must try to settle in existing groups may also be revealing. Focusing further studies on variation in the benefits of sociality for individuals within a species, including humans, may produce more evidence that all individuals do not benefit equally from maintaining strong social relationships; a provocative suggestion that requires further study.

Ethics. Marmots were studied under annual permits issued by the Colorado Division of Wildlife (TR-917). All procedures were approved under research protocol ARC 2001-191-01 by the University of California Los Angeles Animal Care Committee on May 13, 2002, and renewed annually.

Data accessibility. Data and analysis code will be uploaded to Dryad upon acceptance.

Author's contributions. D.T.B. conceived idea and designed analyses with J.G.A.M., D.M.W., and A.L. D.T.B., D.M.W., S.K., and J.G.A.M. collected the data. J.G.A.M., D.M.W., and A.L. analysed the data. All authors interpreted the data and contributed to manuscript writing.

Competing interests. We declare we have no competing interests.

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References

[1] Carey JR. 2003 *Longevity: The Biology and Demography of Life Span*. Princeton, NJ: Princeton University Press.

[2] Hoenig JM. 2005 *Empirical Use of Longevity Data to Estimate Mortality Rates*. SEDAR33-RD17. SEDAR, North Charleston, SC. 8.

[3] Umberson D, Montez JK. 2011 Social relationships and health: A Flashpoint for Health Policy. *J. Health. Soc. Behav*. 51, S54-S66.

[4] Cusumano-Towner M, Li DY, Tuo S, Krishnan G, Maslove DM. 2013 A social network of hospital acquired infection built from electronic medical record data. *J. Am. Med. Inform. Assoc*. 20, 427-434.

[5] Yang YC, Boen C, Gerken K, Li T, Schorpp K. Harris KM. 2014 Social relationships and physiological determinants of longevity across the human life span. *Proc. Nat. Acad. Sci. USA*. 113, 578-583.

[6] Holt-Lunstad K, Smith TB, Layton JB. 2010 Social relationships and mortality risk: a meta-analytic review. *PLoS Med*. 7, e1000316,

[7] Thoits PA. 2011 Mechanisms linking social ties and support to physical and mental health. *J. Health Soc. Behav*. 52, 145-161.

[8] McCowan B, Beisner B, Bliss-Moreau E, Vandeleest J, Jin J, Hannibal D, Hsieh F. 2016 Connections matter: social networks and lifespan health in primate translational models. *Front Psychol*. 7, 433.

[9] Althubaiti A. Information bias in health research: definition, pitfalls, and adjustment methods. *J. Multidiscip. Healthc*. 9, 211-217.

[10] Silk JB, Beehner JC, Bergmann TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010 Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* 20, 1359-1361.

[11] Brent LJN, Ruiz-Lambides A, Platt ML. 2017 Family networks size and survival across the lifespan of female macaques. *Proc. R. Soc. B*. 284: 20170701.

[12] Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D.W. and Pelletier, F., 2015. Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. *Ecology*. 96, 631-641.

[13] Barocas A, Ilany A, Koren L, Kam M, Geffen E. 2011 Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE*. 6: e22375.

[14] Stanton MA, Mann J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS ONE*. 7: e47508.

[15] Kappeler PM, Cremer S, Nunn CL. 2015 Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. *Phil. Trans. R. Soc. B*. 370, 20140116.

[16] Blumstein DT. 2013 Yellow-bellied marmots: insights from an emergent view of sociality. *Phil. Trans. R. Soc. B*. 368, 20120349.

[17] Armitage KB. 2014 *Marmot Biology: Sociality, Individual Fitness, and Population Dynamics*. Cambridge University Press, Cambridge.

[18] Lea AJ, Blumstein DT, Wey TW, Martin JGA. 2010 Heritable victimization and the benefits of agonistic relationships. *Proc. Nat. Acad. Sci.* USA. 107, 21587-21592.

[19] Wey TW, Blumstein DT. 2012 Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behav. Ecol. Sociobiol*. 66, 1075-1085.

[20] Yang WJ, Maldonado-Chaparro A, Blumstein DT. 2017 A cost of being amicable in a hibernating marmot. *Behav. Ecol.* 28, 11-19

[21] Blumstein DT, Wey TW, Tang K. 2009 A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. R. Soc. B* 276, 3007-3012.

[22] Blumstein DT, Ozgul A, Yovovitch V, Van Vuren DH, Armitage KB. 2006 Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *J. Zool. Lond.* 270, 132-138.

[23] DT Blumstein, unpublished observations.

[24] Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson ST, Coulson T. 2010 Coupled dynamics of body mass and population growth in response to environmental change. *Nature*. 466, 482-485.

[25] Lavretsky H, Newhouse PA. 2012. Stress, inflammation and aging. *Am. J. Geriatr. Psychiatry 20*, 729-733.

[26] Blumstein DT, Patton ML, Saltzman W. 2006 Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biol. Lett.* 2, 29-32.

[27] Smith JE, Monclús R, Wantuck D, Florant GL, Blumstein DT. 2012 Fecal glucocorticoid metabolites in wild yellow-bellied marmots: experimental validation, individual differences and ecological correlates. *Gen. Comp. Endocrinol.* 178, 417-426.

[28] Huang B, Wey TW, Blumstein DT. 2011 Correlates and consequences of dominance in a social rodent. *Ethology*. 117, 573-585.

[29] Fuong H, Maldonado-Chaparro A, Blumstein DT. 2015 Are social attributes associated with alarm calling propensity. *Behav. Ecol*. 26, 587-592.

[30] Csardi G, Nepusz T. 2006 The igraph software package for complex network research. *Int. J. Complex Syst.* 1695.

[31] R Core Team. 2016 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

[32] Wasserman S, Faust K. 1994 *Social Network Analysis: Methods and Application*. New York, NY: Cambridge University Press.

[33] Wey T, Blumstein DT, Shen W, Jordan, F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75, 333-344.

[34] Barrat, A, Barthelemy, M, Pastor-Satorras, R, Vespignani, A. 2004 The architecture of complex weighted networks. *Proc. Nat. Acad. Sci.* USA. 101, 3747-3752.

[35] Newman MEJ. 2010 Networks: An Introduction. Oxford, U.K.: Oxford University Press.

[36] Hadfield JD. 2010 MCMC methods for multi–response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Soft*. 33, 1–22.

[37] Yang YC, Boen C, Gerken K, Schorpp K, Harris KM. 2016 Social relationships and physiological determinants of longevity across the human life span. *Proc. Nat. Acad. Sci.* USA. 113, 578-583.

[38] Wey TW, Blumstein DT. 2010 Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim. Behav*. 79, 1343-1352.

[39] Yang WJ, Maldonado-Chaparro AA, Blumstein DT. In review. Identifying the behavioral rules underlying social network structure in yellow-bellied marmots (*Marmota flaviventer*). *Ecol. Model.*

[40] Lea AJ, Blumstein DT, Wey TW, Martin JGA. 2010 Heritable victimization and the benefits of agonistic relationships. *Proc. Nat. Acad. Sci.* USA. 107, 21587–21592.

[41] Higashi M, Yamamura N. 1994. Resolution of evolutionary conflict: a general theory and its applications. *Pop. Ecol. Rev.* 36, 15-22.

[42] Giraldeau L, Caraco T. 2000 *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

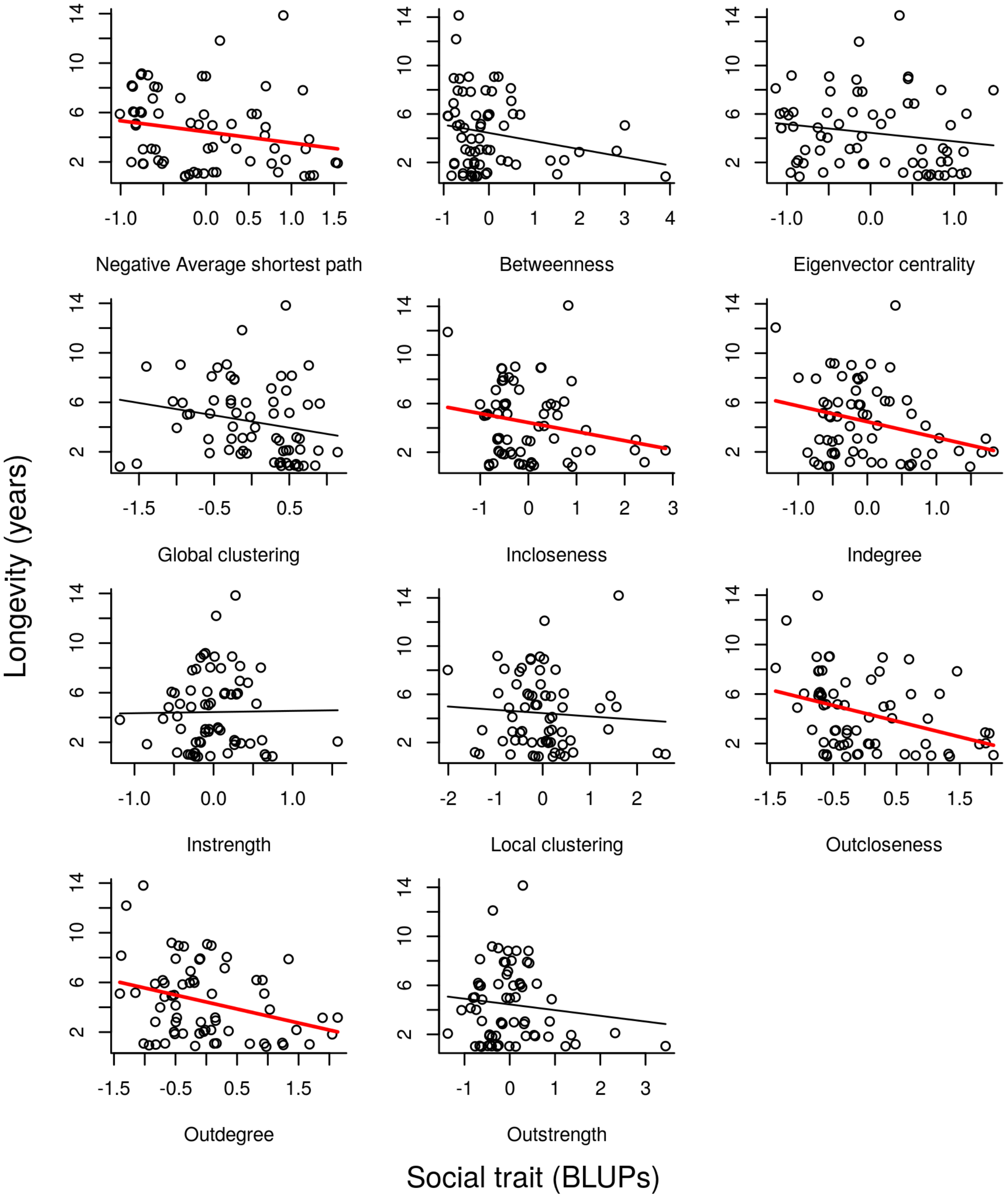
Table 1. Fixed effects fitted on social network traits within bivariate models of social network traits and longevity. Down valley was used as a reference level. We report estimates with lower and upper 95% credible intervals between parentheses. Estimates in bold were significantly different from zero.

Social network trait	Intercept	Faecal Glucocorticoid Metabolites	Age	Position in Valley [up]
Negative average shortest path	**0.425 (-0.064/0.929)**	0.100 (-0.021/0.217)	0.028 (-0.033/0.089)	-0.376 (-0.785/0.055)
Betweenness	0.524 (-0.023/1.071)	-0.135 (-0.309/0.045)	-0.005 (-0.081/0.074)	-0.409 (-0.970/0.158)
Eigenvector centrality	**0.564 (0.022/1.0787)**	0.066 (-0.113/0.247)	**-0.114 (-0.186/-0.044)**	0.058 (-0.401/0.548)
Global clustering	-0.352 (-0.805/0.0971)	-0.141 (-0.331/0.049)	0.0211 (-0.048/0.090)	**0.471 (0.015/0.906)**
Incloseness	**0.855 (0.201/1.484)**	-0.013 (-0.140/0.116)	-0.025 (-0.097/0.048)	-0.336 (-0.828/0.150)
Indegree	**0.873 (0.293/1.484)**	-0.067 (-0.243/0.106)	-0.071 (-0.139/0.001)	-0.262 (-0.692/0.199)
Instrength	0.429 (-0.164/1.010)	-0.043 (-0.239/0.140)	-0.080 (-0.140/-0.020)	-0.126 (-0.484/0.230)
Local clustering	-0.286 (-1.179/0.651)	-0.124 (-0.306/0.050)	0.135 (0.051/0.225)	0.261 (-0.304/0.864)
Outcloseness	0.594 (-0.037/1.185)	-0.005 (-0.131/0.110)	0.019 (-0.053/0.091)	-0.198 (-0.687/0.289)
Outdegree	0.414 (-0.0860/0.903)	-0.048 (-0.212/0.111)	0.005 (-0.070/0.071)	-0.151 (-0.648/0.354)
Outstrength	0.507 (-0.004/1.071)	-0.071 (-0.251/0.115)	-0.062 (-0.138/0.018)	-0.341 (-0.829/0.168)

Table 2. Results of bivariate models illustrating the variance, covariance and correlation at the individual level between longevity and weighted affiliative social traits. We report the estimates with lower and upper 95% credible intervals between parentheses. Estimates in bold were significantly different from zero.

Social network trait	V_{SNT}	$V_{longevity}$	Correlation
Negative average shortest path	0.620 (0.385/0.882)	0.356 (0.222/0.507)	**-0.417 (-0.636/-0.103)**
Betweenness	1.106 (0.662/1.607)	0.358 (0.226/0.509)	-0.280 (-0.525/0.002)
Eigenvector centrality	0.732 (0.431/1.091)	0.372 (0.231/0.528)	-0.277 (-0.545/0.016)
Global clustering	0.584 (0.314/0.901)	0.360 (0.219/0.513)	-0.117 (-0.472/0.153)
Incloseness	0.887 (0.550/1.257)	0.346 (0.215/0.492)	**-0.493 (-0.667/-0.183)**
Indegree	0.622 (0.341/0.955)	0.362 (0.228/0.509)	**-0.393 (-0.650/-0.138)**
Instrength	0.308 (0.136/0.499)	0.361 (0.230/0.517)	0.120 (-0.220/0.448)
Local clustering	0.976 (0.543/1.482)	0.369 (0.230/0.525)	-0.0539 (-0.364/0.309)
Outcloseness	0.864 (0.555/1.211)	0.346 (0.214/0.491)	**-0.596 (-0.778/-0.378)**
Outdegree	0.875 (0.536/1.256)	0.351 (0.219/0.501)	**-0.462 (-0.686/-0.195)**
Outstrength	0.795 (0.431/1.195)	0.365 (0.229/0.516)	0.0165 (-0.247/0.358)

Figure 1. Relationship between social network traits and longevity in yellow-bellied marmots. Best linear unbiased predictors (BLUPs) were used for social network traits for illustrative purposes. Each point represents an individual. Lines represent the relation between social trait and longevity, estimated as the linear regression between social trait BLUP and longevity. Bold red lines are significantly different from zero according to Table 1.



Supplementary Table S1 Results of bivariate models illustrating the covariance between longevity and unweighted affiliative social attributes after controlling for random effects including marmot identity, birth year, and colony and the fixed effects of fecal glucocorticoid levels (ng/g) and age. We report estimates with lower and upper 95% credible intervals between parentheses. Estimates in bold were significantly different from zero.

Social network trait	V_{SNT}	$V_{longevity}$	Correlation
Negative average shortest path	0.617 (0.385/0.885)	0.357 (0.219/0.505)	**-0.371 (-0.638/-0.101)**
Betweenness	1.104 (0.653/1.610)	0.369 (0.231/0.528)	**-0.307 (-0.536/-0.00553)**
Eigenvector centrality	0.711 (0.432/1.030)	0.336 (0.216/0.472)	-0.0714 (-0.379/0.219)
Global clustering	0.583 (0.300/0.887)	0.364 (0.230/0.517)	-0.193 (-0.477/0.152)
Incloseness	0.888 (0.556/1.2721)	0.332 (0.212/0.466)	**-0.443 (-0.676/-0.199)**
Indegree	0.621 (0.327/0.941)	0.356 (0.226/0.507)	**-0.397 (-0.637/-0.114)**
Local clustering	0.9766 (0.552/1.482)	0.341 (0.218/0.491)	-0.0350 (-0.38111/0.296)
Outcloseness	0.870 (0.555/1.229)	0.362 (0.229/0.518)	**-0.601 (-0.759/-0.354)**
Outdegree	0.874 (0.527/1.246)	0.353 (0.216/0.505)	**-0.506 (-0.694/-0.201)**

Supplementary Table S2. Variance components for bivariate models of social network traits (SNT) and longevity with their 95% credible intervals between parentheses. Year and cohort were fitted only on social traits and longevity respectively. V_R is the residual variance estimated for social network traits. Residual variance of longevity was fixed at zero in the bivariate model.

Social network trait	SNT: V_{year}	SNT: V_R	Longevity: V_{cohort}
Negative average shortest path	0.373 (0.103/0.784)	0.180 (0.151/0.212)	0.859 (0.222/1.708)
Betweenness	0.264 (0.0299/0.617)	0.384 (0.320/0.455)	0.819 (0.241/1.677)
Eigenvector centrality	0.338 (0.0664/0.749)	0.433 (0.364/0.512)	0.821 (0.221/1.652)
Global clustering	0.174 (0.0228/0.411)	0.509 (0.422/0.600)	0.819 (0.224/1.667)
Incloseness	0.689 (0.176/1.450)	0.207 (0.175/0.244)	0.829 (0.218/1.639)
Indegree	0.590 (0.122/1.311)	0.394 (0.329/0.464)	0.792 (0.223/1.598)
Instrength	0.678 (0.171/1.465)	0.501 (0.417/0.591)	0.835 (0.232/1.709)
Local clustering	1.725 (0.372/3.77)	0.299 (0.237/0.361)	0.834 (0.226/1.697)
Outcloseness	0.617 (0.163/1.316)	0.187 (0.157/0.220)	0.772 (0.223/1.532)
Outdegree	0.243 (0.0427/0.554)	0.328 (0.276/0.385)	0.771 (0.231/1.563)
Outstrength	0.343 (0.0567/0.763)	0.464 (0.382/0.544)	0.841 (0.213/1.678)

Supplementary Table S3. Fixed effects fitted on longevity within bivariate models of social network traits and longevity. Down valley was used as a reference level. We report estimates with lower and upper 95% credible intervals between parentheses.

Social network trait	Intercept	Valley[up]
Negative average shortest path	-0.177 (-0.391/0.701)	0.245 (-0.113/0.614)
Betweenness	0.135 (-0.384/0.688)	0.211 (-0.150/0.576)
Eigenvector centrality	0.140 (-0.429/0.674)	0.232 (-0.138/0.606)
Global clustering	0.169 (-0.380/0.721)	0.190 (-0.178/0.559)
Incloseness	0.171 (-0.359/0.721)	0.178 (-0.184/0.530)
Indegree	0.151 (-0.407/0.678)	0.196 (-0.172/0.557)
Instrength	0.170 (-0.345/0.745)	0.178 (-0.187/0.548)
Local clustering	0.160 (-0.360/0.744)	0.190 (-0.199/0.561)
Outcloseness	0.106 (-0.398/0.638)	0.279 (-0.0635/0.629)
Outdegree	0.140 (-0.387/0.656)	0.231 (-0.135/0.582)
Outstrength	0.171 (-0.367/0.737)	0.182 (-0.188/0.553)