Agonistic and affiliative social relationships are associated with marmot docility but not boldness

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All animals must face predation risks at some points in their lives and individuals may vary in how much risk they are willing to accept. While it is well recognized that sociality is a way to manage risks, and social group size effects are well studied, the specific ways in which different types of social relationships influence individual risk response, such as number of interaction partners or the centrality of an individual's position in their group, are not well understood. We examined how yellow-bellied marmots, *Marmota flaviventer*, affiliative and agonistic social networks are associated with two repeatable measures of risk-related behaviour: boldness/risk taking, quantified from flight initiation distance to a simulated predator approach, and docility/risk aversion, quantified from response to human trapping and handling. We found that docile individuals were less socially integrated and that certain agonistic, but not affiliative, social network measures that quantified their positions in their networks were associated with individual docility. Animals in tighter agonistic networks were also those who were less docile after controlling for a number of other variables that could explain variation in these traits. We found that boldness was not correlated with an individual's agonistic or affiliative interactions. We conclude that some social network measures are part of a docility syndrome in yellow-bellied marmots. Similar studies in other systems are needed to better understand the importance of agonistic and affiliative relationships in selecting for behavioural syndromes.
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Animals must take a variety of risks to survive and may respond to risk in consistent ways. Individuals vary in their behavioural types or personalities, which are defined as consistent among-individual differences in behaviour (Sih & Bell, 2008), and these may be associated with how they manage risks. Personality traits, such as boldness, aggression, exploration and sociability, can have fitness consequences (reproductive success: Smith & Blumstein, 2008; survival: Moiron et al., 2020) and are often associated with dominance rank (Bibi et al., 2019; Colléter & Brown, 2011; Ramos et al., 2021) and invasion potential (Chapple et al., 2012). Furthermore, there may be carryover effects of behaviours between situations, such as when individuals with high social aggression also

engage in high levels of aggression against predators, creating a behavioural syndrome (Sih et al., 2004, van Oers et al., 2005). Both personality types and behavioural syndromes can be shaped by multiple factors, including external stimuli or individual experiences (Smith & Blumstein, 2013; Wolf & Weissing, 2012). For instance, threespine sticklebacks, *Gasterosteus aculeatus*, only develop an aggression syndrome between social aggression and aggression against predators after they have been exposed to predators (Bell & Sih, 2007; Herczeg et al., 2009). Other factors such as familiarity and size of conspecifics (Conrad et al., 2011) or group size (Piyapong et al., 2010) can also alter the adaptive value and structure of a behavioural syndrome.

Sociality is one external factor that may be associated with the way individuals behave. Specific relationships and hierarchies within a group may lead to unequal distribution of social benefits, driving individual variation in behavioural responses to risk—reward trade-offs. Alternatively, individuals who consistently behave in risky ways may find themselves in certain social

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positions, as seen when bolder individuals have higher dominance ranks than shyer individuals (Mettler & Shivik, 2007; Sasaki et al., 2018; but see Padovani et al., 2021). Importantly, this suggests that risk management may inform or be shaped by an individual's social environment.

The social environment may provide benefits such as protection from predators (Caro, 2005; Guindre-Parker & Rubenstein, 2020; Hamilton, 1971) and create a sense of social security (Mady & Blumstein, 2017). Female elk, *Cervus elaphus*, are more vigilant when they occupy an edge position in a herd, are in a smaller herd and during calving season (Lung & Childress, 2007). Stronger affiliative relationships can also provide benefits including improved health outcomes (Jablonski, 2021; Umberson & Montez, 2011). Alternatively, the social environment can lead to costs such as increased competition for resources (Bolnick & Preisser, 2005; Hamilton, 2004; Kilgour et al., 2018). Male elk primarily increase vigilance to account for conspecific risk or aggression during breeding season (Lung & Childress, 2007). Dominant vervet monkeys, *Chlorocebus pygerythrus*, forage along the edges of groups where they are more likely to encounter and monopolize food sources but are also more likely to encounter predators (Teichroeb et al., 2015). Alternatively, individuals subjected to aggression from conspecifics, who are often of low rank and otherwise excluded from accessing resources, may also show increased risk-taking behaviour (Giraldeau & Caraco, 2018; Goss-Custard, 1980).

The mechanisms driving this relationship between risk-taking behaviour and sociality are complicated and may involve different and potentially opposing mechanisms. To properly investigate this relationship, different aspects of sociality must be quantitatively studied. Social networks visualize and quantify an individual's social relationships, including specific measures, such as the amount of contact between two individuals or how central an individual is to their network. Social networks can be built from different types of social interactions, such as affiliative versus aggressive interactions, which may be associated with individual behaviour in different ways (Díaz López, 2020; Snijders et al., 2014).

Social network measures quantify relationships beyond simple dyadic interactions allowing researchers to assess specific facets or what might be viewed as attributes of social behaviour (Blumstein, 2013; Croft et al., 2008; Pinter-Wollman et al., 2014; Wey et al., 2008). For instance, relationship strength, the number of interactions occurring between two individuals, is associated with the likelihood of engaging in predator inspection, latency to return to foraging after alarm calls and reactivity to a threat (Blumstein et al., 2017; Croft et al., 2006; Nadler et al., 2021). It is important to study how these aspects of social interactions correlate with external pressures, such as predation, dominance and food competition, because individual differences in behaviour inform or are shaped by social relationships and likely influence the adaptive value of sociality.

Yellow-bellied marmots (hereafter, marmots) are a ground-dwelling sciurid rodent that have been well studied in the wild (Armitage, 2014; Blumstein, 2013). Marmots are facultatively social and, contrary to most social mammals, experience largely negative effects of strong affiliative relationships including decreased reproductive success and longevity (potentially due to costs of maintaining affiliative relationships or negative density effects) and decreased overwinter survival (potentially due to asynchronous torpor bouts) (Blumstein et al., 2018; Wey & Blumstein, 2012; Yang et al., 2016). However, marmots benefit from sociality overall through predator detection and alarm calling (Montero et al., 2020). Social groups are composed of closely related matrilines, and yearlings engage in the majority of affiliative behaviours that hold groups together, while older female marmots become more agonistic as they age (Wey & Blumstein, 2010). The complex effects

of affiliative and agonistic sociality make them an ideal species in which to study the interaction between individually distinctive risk-taking behaviour and social network measures.

Marmots exhibit consistent individual differences in both boldness, measured from flight initiation distance, and docility, measured as reactivity to trapping, across life stages as yearlings and adults, but the two personality traits together do not form a syndrome (Petelle et al., 2013). Previously, defensive aggression, a measure related to docility and defined as a principal component composed of struggling and biting while in a trap, was found to not correlate with measures of agonistic sociality, including measures of the tendency to initiate or receive aggression, suggesting that aggression against predators and social aggression may evolve separately (Blumstein, Petelle et al., 2013). Defensive aggression was also not state dependent but did have positive feedbacks from mass and age (Petelle et al., 2019).

Here we use Bayesian bivariate models to expand on previous work on marmot personalities to determine whether there is an association between specific social network measures in affiliative and agonistic contexts and two individually repeatable measures: boldness (a risk-taking behaviour calculated from flight initiation distance) and docility (a risk-averse behaviour inferred from the response to trapping and handling).

Overall, we hypothesized that affiliative interactions provide social security benefits and agonistic interactions are associated with resource competition. Thus, bold (risk taking) and docile (risk averse) personalities could be positively correlated with affiliative interactions. Although bold (risk taking) personalities could be positively associated with agonistic interactions, we expected docility (risk-averse) to be negatively associated with agonistic interactions.

By separately analysing affiliative and agonistic network measures, we can potentially infer how these different measures of social relationships are associated with individually specific risk taking. While we were able to make general predictions, we acknowledge that our study was exploratory, given that we did not know which social network measures, if any, would be significantly associated with personality traits. Thus, we formally analysed multiple social network measures, in a structured way, to reveal how different components of sociality relate to personality traits.

METHODS

Study Site and Species

We studied yellow-bellied marmots in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, U.S.A. (38°57′38″N, 106°59′14″W). Marmots have been studied in this location since 1962 (Armitage, 2014), but we focused our analyses on data collected between 2003 and 2019, an interval during which we focused intensively on collecting social interaction data. Yellow-bellied marmots live in matrilineal social groups and usually occupy subalpine slopes and meadows (Armitage, 2014; Frase & Hoffmann, 1980). Colonies can be composed of multiple social groups that vary in composition and size. Our primary study site was the Upper East River Valley, which is divided into up- and down-valley sites that differ in the length of their winter by a few weeks (measured by the date at which 50% of the snow melts out of a colony site) and hence the duration of their summer growing season (Van Vuren & Armitage, 1991). Overall, we observed 12 separate colonies spread over 5 km. Colonies were defined by physical separation of a minimum of 200 m or an intervening physical feature, such as a river. The Upper East River Valley is subjected to human influences from tourism and research. Some colonies occur in close proximity to humans, with burrows being

built under occupied rustic cabins. Marmots have also become more tolerant of tourist-related human disturbance over time (Morgan et al., 2021) and have individually habituated or sensitized to research-related human disturbance (Uchida & Blumstein, 2021).

We had a biweekly trapping schedule where each colony was trapped one to two times every other week using Tomahawk live traps baited with molasses horse feed (Omalene 100, Ralston Purina, St Louis, MO, U.S.A.). Individuals who were trapped were permanently marked with unique individual eartags, and we applied fur marks to their dorsal pelage using nontoxic Nyanzol-D dye to aid in identification from afar (Blumstein et al., 2009). All individuals included in this study were trapped at least once a year or were otherwise individually identifiable by unique physical markings. Weather permitting, we quantified social observations through all occurrence sampling on marmot colonies during peak activity (0700–1100 hours and 1600–1900 hours) between mid-April and September with binoculars and 15–45× spotting scopes.

Quantifying Behavioural Traits and Other Correlates

Boldness

Following Petelle et al. (2013), we quantified boldness from the inverse of the flight initiation distance (FID): bold animals tolerated closer approach than shy animals. Flight initiation distance is the distance at which an animal begins to flee after alerting to an approaching threat (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986) and can be used to measure risk taking, whereby individuals with larger flight initiation distances prioritize safety over rewards, such as foraging or potential mating opportunities. Between 2003 and 2019, we recorded marmot flight initiation distance during simulated predator approaches. The researcher would arrive at a colony and wait quietly for a minimum of 10 min to ensure the animals were relaxed. After identifying the target individual (targeted based on data abundance), the researcher walked at a measured pace of 0.5 m/s towards the subject. The researcher dropped a flag to mark their starting distance, the target individual's alert distance and its flight initiation distance. Alert distance was the distance at which the target individual became vigilant, noted as obvious turning of body or head towards researcher. Alert distance was noted because it explains significant variation in FID (Blumstein et al., 2016). Flight initiation distance was the distance between the researcher and the animal when the marmot fled (Frid & Dill, 2002). An individual's flight initiation distance was measured a median of three times per season (first quartile: 2; third quartile: 5), with a range of one to nine trials in all data sets. FIDs were collected over a period of 12–15 weeks and typically no more than one FID was taken on an individual per day. Distance to burrow, the distance between the subject's initial location and the burrow in which it escaped, were also recorded to account for other factors that could influence risk assessment.

Docility

Docility is a metric of risk in that the most docile individuals are considered the most compliant or risk averse (Careau et al., 2010; Réale et al., 2007; Westrick et al., 2019). Previous studies in the yellow-bellied marmot system have shown that individuals who struggle in a trap have increased glucocorticoid levels (Smith et al., 2012), indicating that there may be a physiological aspect to docility. Following previous definitions of docility (Petelle et al., 2013, 2013, 2019, 2013; Réale et al., 2000), we calculated docility as the sum of a suite of behavioural responses to trapping. An individual's docility was composed of five behaviours dichotomously scored (i.e. 0/1) while trapping: alarm calling, tooth chattering, struggling in the trap, biting the cage and attempting to escape by immediately entering the handling bag (Petelle et al., 2013, 2019). During trapping, the observer first approached the trap and set up data collection materials (<1 min). Afterwards, a conical cloth bag was affixed around the trap entrance and the door was opened, allowing the marmot to enter the bag. 'Entering the handling bag' was scored as 1 if the individual immediately ran or walked into the bag upon opening of the door and scored as 0 if the individual took longer to enter the bag. Throughout the encounter, from first approach to release of the individual, the observers noted the occurrence of any alarm calling, tooth chattering, struggling in the trap (any movement beyond shifting position) and biting the cage. These behaviours were scored as 1 if they occurred even once during the encounter and as 0 if the behaviour was never exhibited during the encounter. The individual's scores for these five behaviours were summed and then subtracted from the maximum potential count (5) to create their docility index score. Thus, the most docile individuals would score 5, whereas the least docile individuals would score 0. Individuals were trapped a median of eight times per season (first quartile: 5; third quartile: 11), with a range of 1–25 trapping events in all data sets. Although an average of four observations per individuals is sufficient to estimate intraindividual consistency in docility in marmots, the number of repeated measurements per individual in our study was much larger than strictly required, because our sampling protocol was designed to estimate short-term and long-term repeatability as well as age specific heritability in both mean and predictability of docility and, thus, required more repeated sampling.

Social network measures

We quantified social observations using all occurrence behaviour sampling in each colony between mid-April and September. Observations were used to create interaction matrices between all individuals within a colony, which were then used to calculate social network measures. To create interaction matrices, we first filtered data for transient individuals (excluded individuals observed <5 times per year), pups (who emerge halfway through the active season) and unknown individuals. The resulting data set consisted of interactions with known initiators and receivers, from which we calculated interaction matrices with directional ties to indicate both connectivity and orientation. Interaction matrices were calculated separately for affiliative behaviours (e.g. play, allogrooming, sitting together) and agonistic behaviours (e.g. fighting; full ethogram in the Appendix, Table A1).

From these interaction matrices, we calculated the following social network measures: degree (in and out), strength (in and out), closeness (in and out), betweenness centrality, eigenvector centrality and local clustering coefficient. Betweenness centrality, in/outcloseness and eigenvector centrality were calculated from unweighted data. Eigenvector centrality was additionally calculated without directional data. Descriptions of all social network measures are in Table 1.

Although agonistic and affiliative interactions are independent behaviours, there was some degree of correlation between social network measures calculated from the two interaction types. Although most social network measures were not highly correlated (<0.5), affiliative and agonistic indegree and outdegree had high correlation indices (>0.5) with each other and with incloseness, outcloseness and to a lesser degree eigenvector centrality. We have included the results of a pairwise Pearson correlation test between all agonistic and affiliative social network measures in the Appendix (Fig. A5). All social network measure analyses were performed in R version 4.1.0 (R Core Team, 2018) with the 'igraph' package version 1.2.4 (Csárdi & Nepusz, 2006). Correlations between social network measures in each data set are provided in the Appendix (Figs A1–A4).

Table 1
Descriptions of social network measures used in this study

Social network measure	Description
Indegree	Numbers of individuals from whom focal individuals received interactions (Wasserman & Faust, 1994)
Outdegree	Number of individuals with whom focal individuals initiated interactions (Wasserman & Faust, 1994)
Instrength	Focal individual received many repeated interactions from others (Wasserman & Faust, 1994)
Outstrength	Focal individual initiated many repeated interactions with others (Wasserman & Faust, 1994)
Incloseness	Focal individual received interactions more directly from others; measured as the inverse of the topological shortest distance between a focal individual and all other individuals in the group (Yang et al., 2016)
Outcloseness	Focal individual initiated interactions with others more directly; measured as the inverse of the topological shortest distance between a focal individual and all other individuals in the group (Yang et al., 2016)
Betweenness centrality	Proportion of shortest path lengths that passed through the focal individual, i.e. bridging of network (Wey et al., 2008)
Eigenvector centrality	Connectedness of focal individual in network taking into account indirect relationships of neighbours (Wasserman & Faust, 1994; Yang et al., 2016)
Local clustering	Cliquishness, a measure of the degree to which individuals were more closely tied to one another than to other members of their network; or individual embeddedness within their network (Yang et al., 2016); calculated as the number of relationships a focal individual had divided by the maximum number of potential relationships (Mady & Blumstein, 2017; Wey et al., 2008)

Ethical Note

Marmots were studied under Animal Research Committee (ARC) protocol 2001-191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR519) and the Rocky Mountain Biological Laboratory's Animal Care Committee (Protocol 1). Live-trapping protocols have been continuously used since 1962, during which time there has been no indication of adverse effects at the population level (population size fluctuates over time). Traps are checked regularly and are not set when it is raining or snowing, or when it is too hot. When inclement weather (e.g. thunderstorms) arose suddenly, animals were released without processing if conditions were unsafe, or they were moved to a dry spot for processing if conditions were safe for animals and people. Traps were shaded to prevent direct sunlight from impacting the animals and were baited. Traps were typically checked after 2–3 h but checked more frequently if temperatures were high (>21 °C) and closed if temperature exceeded 24 °C. Water was not provided in traps due to the short duration of the trapping interval and because marmots get most of their water from eating natural vegetation. Once we got to a trap, marmots were processed without anaesthesia within 5–15 min (depending upon what was required) and released at their point of capture. Researchers decreased stress for the animals by avoiding sudden movement and by talking quietly during processing and did not approach trapped individuals until they were to be processed. Individuals that were excessively stressed were released with minimal or no processing, depending upon their condition. Flight initiation distances have been studied since 2003 and create a minimal distraction; marmots that flee to their burrows resume normal behaviour, weather permitting, soon after we left the area. Observations were conducted at distances that did not interfere with natural behaviour, which varies by group. Our overall goal was to not interfere with the population biology of these animals. We support a culture to improve the welfare associated with all that we do. Over time, trapping and handling strategies have been modified, based on suggestions from personnel, to be more efficient and, ultimately, less disruptive.

Statistical Analysis

We determined the adjusted repeatability of boldness and docility traits using the 'rptGaussian' function in the 'rptR' package (Stoffel et al., 2017) with nboot = 1000 and nperm = 1000. We fitted the boldness trait repeatability models with age category, sex, colony, relative dominance rank, yearly predator index, distance to burrow during FID, alert distance, days between FID events at a colony, the number of FID events at a colony during a year and the time of day of FID event (morning/afternoon) as fixed effects and unique individual identity and year as random effects. We fitted the docility trait repeatability models with age category, sex, colony, relative dominance rank, yearly predator index, days between trapping events at a colony, the number of trapping events at a colony during a year and the time of day of trapping event (morning/afternoon) as fixed effects and unique individual identity and year as random effects.

To test the relationship between boldness or docility and each of the social network measures, we fitted a series of bivariate generalized linear mixed-effects models of boldness or docility and nine different social network measures. Each of these models fitted two dependent variables: one social network measure and one of the two personality traits. We created four data sets, each with a unique combination of docility or boldness and affiliative or agonistic social network measures (i.e. agonistic social network measures and docility from one of the four data sets). All models included the random effects of marmot identity and year to account for individual and annual variation. Bivariate models allow specification of different fixed effects on each of the dependent variables. To account for individual and environmental effects on sociality and personality, we fitted age category (yearling, adult), sex, predator index, relative dominance rank and colony as fixed effects on both the social network measure and personality trait. To control for habituation effects from the data collection methods for the two personality traits, we fitted days between trapping events at a colony, the number of trapping events at a colony per year and the time of day of trapping event (morning/afternoon) as fixed effects on docility and days between FID measurements at a colony, number of FIDs within a year at each colony and time of day FID (morning/afternoon) as fixed effects on boldness. Additionally, we fitted alert distance and distance to burrow as fixed effects on boldness to account for expected variation in FIDs. All continuous variables were centred and scaled with a mean of zero and a variance of one to permit comparison across traits. Prior to fitting bivariate models, we fitted univariate models for each trait using a Gaussian distribution and verified model assumptions (linearity, homoscedasticity, normality and independence of residuals and collinearity) for each trait separately.

We fitted bivariate generalized linear mixed-effects models using Markov chain Monte Carlo techniques under a Bayesian approach with the 'MCMCglmm' package (Hadfield, 2010) in R. We used priors at the correlation level for individual identity effect (i.e. parameter expanded prior: $V = \text{diag} (2) \times 0.02$, $\mu = 3$, $\alpha.\mu = \text{rep} (0,2)$, $\alpha.V = \text{diag} (2) \times 1000$). The priors for year random effects were weakly informative ($V = 1$ and $\mu = 0.002$), and the prior for the residual variance was weakly informative for social measures ($V = \text{diag} (2)$, $n\mu = 1.002$). Each bivariate model was run for 10 000 000 iterations ('nitt'), excluding the first 5000 iterations ('burn-in') and cataloguing one in every 100 runs ('thin'). We examined the trace plots, autocorrelation (<0.05) and effective

sample size (>800) for each estimate to check for convergence and proper mixing of the MCMC chain. All parameters passed the Heidelberg test for parameter convergence. All statistical analyses were performed in R version 4.1.0 (R Core Team, 2018). Additionally, Bayesian models do not typically correct for multiple testing because uninformed or weakly informed priors make it harder to identify relationships and, thus, form a type of control for multiple comparisons (Gelman et al., 2012).

RESULTS

Adjusted repeatability analysis revealed relatively low but significant repeatability for both the boldness trait (affiliative data set repeatability: $R = 0.136$, CI = 0.008−0.312, SE = 0.076, $P = 0.084$; agonistic data set repeatability: $R = 0.133$, CI = 0.013−0.305, SE = 0.075, $P = 0.088$) and the docility trait (affiliative data set repeatability: $R = 0.198$, CI = 0.15−0.245, SE = 0.024, $P < 0.001$; agonistic data set repeatability: $R = 0.193$, CI = 0.146−0.243, SE = 0.025, $P < 0.001$) (repeatability thresholds reviewed in Bell et al., 2009). The agonistic−boldness data set consisted of 566 observations of 166 individuals. The agonistic−docility data set consisted of 3229 observations of 342 individuals. The affiliative−boldness data set consisted of 562 observations on 165 individuals. The affiliative−docility data set consisted of 3170 observations of 340 individuals.

After controlling for known relevant fixed and random effects of risk response behaviour and social measures, we found that there was no association between bold individuals and their social network measures in either the affiliative network (all credible intervals included 0; Fig. 1a, full results in the Appendix, Table A2) or the agonistic network (Fig. 1b, full results in the Appendix, Table A3). There was additionally no general pattern in the direction of these correlations, with only 10 out of 18 models having a negative correlation.

Docile individuals were also those who had lower affiliative outdegree, outcloseness and eigenvector centrality network measures (Fig. 2a, full results in the Appendix, Table A4) and lower agonistic outdegree, instrength, outcloseness and eigenvector centrality (Fig. 2b, full results in the Appendix, Table A5). Additionally, 17 out of 18 models had a negative correlation between docile individuals and their social network measures, with seven of these models having a nonzero negative effect, suggesting that this may be an overall trend.

We include a more detailed discussion of the fixed effects results in the Appendix. Briefly, the number of events (trapping or FID experiments) per year per colony, a potential driver of habituation, was negatively correlated with docility in individuals. Thus, individuals were less docile at colonies that experienced more trapping events during a given year. Boldness, however, was not associated with the number of FID experiments conducted.

DISCUSSION

Our results did not support our initial predictions that both bold and docile personalities would be positively correlated with an individual's affiliative social network measures. Even though affiliative network measures did not form a syndrome with boldness and some affiliative network measures were associated with docility, the direction of these associations were opposite to our expectations. More docile individuals were less socially integrated with their affiliative networks. Specifically, more docile individuals were also those who initiated affiliative interactions with fewer other individuals (outdegree), had less direct interactions (outcloseness) and were less influential in their group (eigenvector centrality). Degree is a measure of direct interactions, while closeness and eigenvector centrality are network measures that reflect an individual's position in the overall social group. However, degree was also correlated with both closeness and eigenvector centrality, indicating that there may be overlap in what specific aspect of social network measures is correlated with docility. Thus, these results suggest that the position of an individual in its social group matters in terms of how docile it is, and from this we can infer a social network measure−docility syndrome.

This result adds to a number of studies identifying the negative or neutral effect of affiliative network measures on yellow-bellied marmots. Previous studies in this species found that social group size, but not the types of affiliative network measures, increases adult female survival against predators (Montero et al., 2020), and that group size, but not the specific measures that compose an individual's position in their social network, explained variation in vigilance (Mady & Blumstein, 2017). Thus, it may be that social network position, per se, does not explain variation in perceptions of security from predators in this species.

These results also provide more evidence that affiliative social network position is likely to influence individual risk-taking behaviour. The formation of social groups is a key antipredator response (Caro, 2005; Hamilton, 1971) and social security provided by affiliative relationships with conspecifics can influence risk taking. Trinidadian guppies, *Poecilia reticulata*, under high predation risk form more stable social relationships (Heathcote et al., 2017), yellow-bellied marmots return to foraging faster after hearing an alarm call from a friendly conspecific (Blumstein et al., 2017) and chimpanzees, *Pan troglodytes schweinfurthii*, alter vigilance depending on whether they have strong affiliative ties with those around them (Kutsukake, 2006).

Our results for boldness similarly did not line up with our initial predictions that bold personalities would be positively associated with agonistic interactions. Instead, we again found that agonistic network measures did not form a syndrome with boldness. However, we predicted that docility would be negatively associated with agonistic interactions. Indeed, more docile individuals were also those who initiated fewer direct agonistic interactions
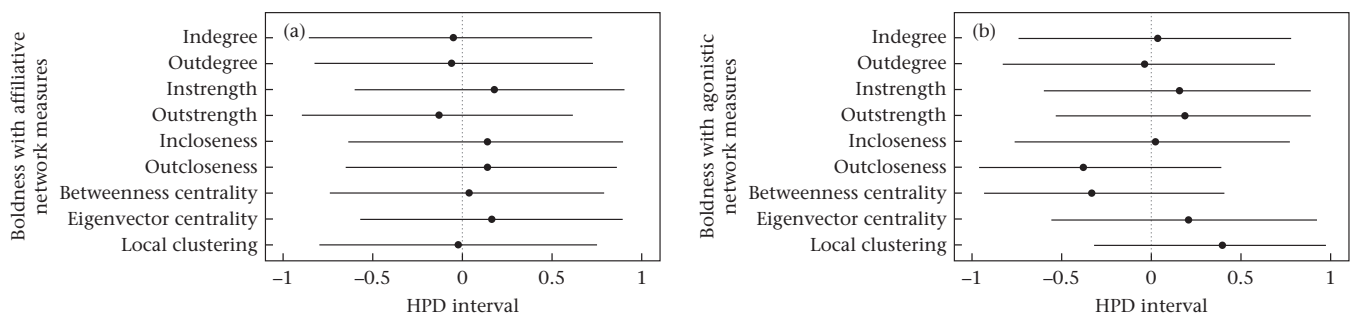
Figure 1. Highest posterior distribution (HPD) intervals of social network measures and boldness. Significant credible intervals do not include 0 (represented by the dotted vertical line). (a) HPD interval for the correlation of boldness and affiliative social network measures. (b) HPD interval for the correlation of boldness and agonistic social network measures.
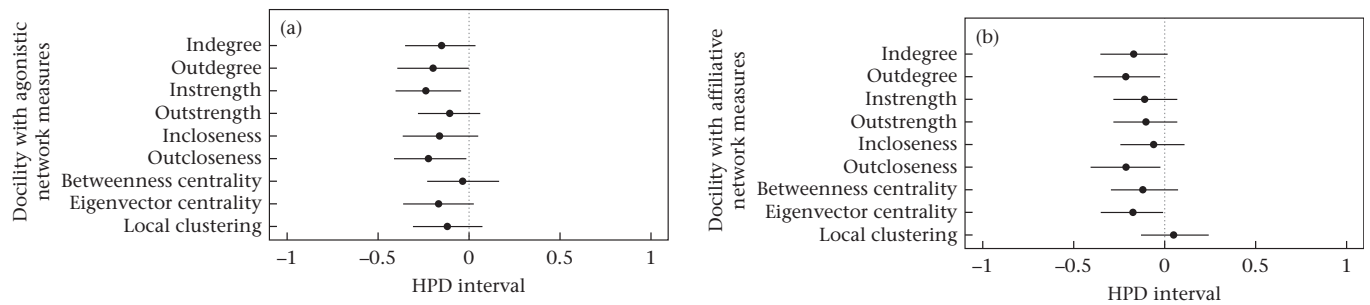
Figure 2. Highest posterior distribution (HPD) intervals of social network measures and docility. Significant credible intervals do not include 0 (represented by the dotted vertical line). (a) HPD interval for the correlation of docility and affiliative social network measures. (b) HPD interval for the correlation of docility and agonistic social network measures.

(outcloseness), initiated agonistic interactions with fewer partners (outdegree), were less influential in their agonistic network (eigenvector centrality) and received fewer agonistic interactions (instrength) overall. Interestingly, a previous study in yellow-bellied marmots found no significant association between social aggression and defensive aggression (a measure related to docility; Blumstein, Petelle et al., 2013). This difference in results may reflect the substantially larger data set we used here; relatively large data sets may be required to identify relatively small effects. Indeed, these new results are expected. While we did not experimentally test for causal relationships, studies in other rodent species have found that socially nonaggressive individuals typically adopt passive or risk-averse response types such as withdrawal or immobility (Benus et al., 1991; Veenema et al., 2005).

The disparity in our docility and boldness results suggest that not all aspects of the social environment influence risk perception. Studies in other species have also used metrics such as speed of exploration in a novel environment or time to resume activity after disturbance to quantify risk management. Fast-exploring great tits, *Parus major*, maintain more central positions in their social network (Snijders et al., 2014), whereas fast-exploring house finches, *Haemorhous mexicanus*, interact more frequently with more conspecifics (Moyers et al., 2018). Moreover, threespine sticklebacks that take more time to resume activity also interact more frequently with fewer individuals (Pike et al., 2008). As such, our results add to a growing literature identifying correlations between a variety of risk-associated behaviours and social network positioning.

Future studies should identify whether there is a causal, directional effect of social interactions on marmot docility. Furthermore, analyses should examine whether docility is associated with less social integration in other species and whether it depends on facultative or obligate social structures. More generally, understanding whether specific social network measures select for docility, or whether the syndrome emerges from some other selective force, would help us better understand the proximate drivers of behavioural syndromes. Similar studies in other systems are needed to better understand the importance of agonistic and affiliative relationships in selecting for behavioural syndromes.

Author Contributions

Conceptualization: D.M.W., S.B. and D.T.B.; Methodology: D.T.B., S.B. and D.M.W.; Investigation: D.M.W., S.B., D.T.B.; Formal analysis: S.B., D.M.W., J.G.A.M.; Writing – original draft: S.B., D.M.W.; Writing – review & editing: D.M.W., S.B., J.G.A.M., D.T.B.; Resources: D.M.W., J.G.A.M. and D.T.B.

Data Availability

Data and R code for this paper are available on the Open Science Framework (OSF) at https://osf.io/a9j24/.

Declaration of Interest

We declare no competing interests.

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Appendix

Additional Methods

Predator index

All predators detected by observers within the study area were recorded, including information on predator species, location (e.g. at a study colony or nearby) and whether the sighting was during observation hours. We first separated these predator observations by year and colony. We then calculated a predator index for each colony each year by dividing the proportion of observation sessions during which a predator was detected at a colony site by the total number of observation sessions at that colony site in a given year. We then determined the predator index from all colonies and all years. We used this value to create a median split. Each colony-year predator index was assigned as high predator pressure or low predator pressure relative to the median predator index. Potential predators (Armitage, 2014) found at our sites were black bears, *Ursula americanus*, mountain lions, *Puma concolor*, coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, badgers, *Taxidia taxus*, red-tailed hawks, *Buteo jamaicensis*, and golden eagles, *Aquila chrysaetos*.

Relative dominance rank

We used the Clutton-Brock index (CBI) to quantify social dominance hierarchies within each year and colony (Clutton-brock et al., 1979). This index calculates a ratio of 'wins' and 'losses' for behavioural interactions, represented by the equation, $CBI = (B + b + 1)/(L + l + 1)$. Here, B is the number of other individuals who 'lost' an interaction to the focal individual (i.e. direct wins of interactions by focal individual), b is the number of individuals who 'lost' to those who 'lost' to the focal individual (i.e. indirect wins of interactions by focal individual), L is the number of others who 'won' an interaction with the focal individual (i.e. direct losses of interactions by focal individual), and l is the number of individuals those 'winners' had 'lost' to (i.e. indirect losses of interactions by focal individual). Unlike other metrics of dominance like David's score (DS) and the frequency-based dominance index (FDI), the CBI does not utilize the rate of interaction in its calculation (Bang et al., 2010). As such, the CBI is more applicable to the study of yellow-bellied marmots because it is suited to a species with low interaction rates (following Blumstein, Chung et al., 2013).

For marmots, 'wins' and 'losses' were recorded for all behavioural interactions. 'Losses' were defined as the individual who moved away from an interaction first. For example, if two individuals were play wrestling, the individual who moved away from the other individual first had 'lost' and the remaining individual was the 'winner'. All interactions with no observable outcome were excluded from calculations. 'Wins' and 'losses' for each individual over the year were recorded in four binary matrices, one for each of the four variables in the CBI. These were then used to calculate a CBI 'win/loss' ratio for each individual and each interaction partner it had.

After calculating these CBI ratios, we computed each individual's relative rank, which accounts for the number of individuals within the hierarchy (Blumstein, Chung et al., 2013; Huang et al., 2011). We first ordered the CBI ratios in each social network from lowest to highest and assigned an absolute rank score based on where an individual was positioned compared to other individuals in their social network. We then divided the absolute rank by the total number of individuals in the social network. The individual with the lowest relative rank in the social network was assigned a zero and the individual with the highest relative rank in the social network was assigned a one. Thus, the most dominant individual would score 1, whereas the least dominant individual would score 0 and all other individuals would fall between 0 and 1.

Results of Fixed Effects

Review of models

Bivariate models allow specification of different fixed effects on each of the dependent variables. Each model fitted age category (yearling, adult), sex, predator index, relative dominance rank and colony as fixed effects on both the social network measure and personality trait. The boldness models fitted days between FID measurements at a colony, number of FIDs within a year at each colony, time of day FID (morning/afternoon), alert distance and distance to burrow as fixed effects. The correlations between boldness and each social network measure are listed in Tables A2—A3. The docility models fitted days between trapping events at a colony, the number of trapping events at a colony during a year and the time of day of trapping event (morning/afternoon) as fixed effects. The correlations between docility and each social network measure are listed in Tables A4—A5.

Fixed effects fitted on social network measures in the boldness data set

In the boldness data set, age category (reference level: adults) was positively correlated with affiliative social network measures and significantly so with betweenness, outcloseness, instrength, outstrength and eigenvector centrality (Table A6). Age category was negatively correlated with most agonistic social network measures

and significantly so with indegree, outdegree, betweenness, incloseness, outcloseness, instrength and outstrength (Table A7). These results suggest that yearlings were more involved with their affiliative networks. Specifically, yearlings were more frequently involved with affiliative interactions, directly initiated these interactions with more members of their groups, bridged different social groups and were more influential in their affiliative networks. Yearlings also had less frequent aggressive interactions with fewer members of their groups, were less likely to initiate interactions directly and were less likely to interact with different agonistic social groups.

Affiliative social network measures were not correlated with sex of the individual (reference level females; Table A6). However, agonistic outdegree and outstrength were positively correlated with sex of the individual (Table A7). Males and females did not differ in their affiliative interactions, but males initiated agonistic interactions more frequently and with more members of their colony than females did.

Affiliative social network measures were positively correlated with predator index, including indegree, outdegree, outstrength, incloseness, outcloseness and local clustering, with the exception of a negative correlation with affiliative betweenness (Table A6). The correlation between agonistic social network measures and predator index was mostly consistent with seven out of the nine models showing a positive direction. Agonistic indegree, eigenvector centrality and instrength were positively correlated with predator index (Table A7). In environments with low predator pressure, individuals had more affiliative interaction partners and interacted more directly with these partners, initiated affiliative interactions more frequently and were more likely to interact in small affiliative cliques. In environments with low predator pressure, affiliative networks were less likely to interact with different social groups. In low predator pressure environments, individuals received more frequent agonistic interactions from more members of their groups and were more influential in their agonistic networks.

Both affiliative and agonistic social network measures had mixed results for their correlations with relative rank. Affiliative betweenness and outcloseness were negatively correlated with relative rank (Table A6). Agonistic indegree and instrength were positively correlated with relative rank, while agonistic eigenvector centrality was negatively correlated with relative rank (Table A7). Low-ranked individuals were also those who were more likely to interact with different affiliative social groups than their high-ranked peers. They were also more influential in their agonistic network. Interestingly, high-ranked individuals were also those who received more frequent aggression from more individuals in their group.

Fixed effects fitted on social network measures in the docility data set

Affiliative and agonistic social network measures were correlated with age category, although the direction of the correlation differed between the two network types. Affiliative social network measures were positively correlated with age category for all measures except betweenness, which was negatively correlated (Table A8). Agonistic social network measures were negatively correlated with age category for all measures except local clustering, which was positively correlated (Table A9). Overall, yearlings were more involved in their affiliative network than adults but they were less likely to interact with different social groups. They were also less likely to be involved in their agonistic network than adults but more likely to be involved with agonistic clusters.

There were few correlations between social network measures and individual sex: affiliative outstrength (Table A8), agonistic outdegree and agonistic outstrength (Table A9) were positively correlated with sex. Thus, males initiated more frequent affiliative interactions and they also initiated agonistic interactions more frequently and against more individuals than females.

Several affiliative social network measures were correlated with predator index. Affiliative indegree, outdegree, incloseness and outcloseness were positively correlated with predator index, while affiliative local clustering was negatively correlated with predator index (Table A8). Agonistic outdegree, instrength, incloseness, outcloseness and local clustering were positively correlated with predator index (Table A9). In low predator pressure environments, individuals had affiliative interactions with more interaction partners and more directly interacted with others. However, low predator pressure also correlated with less well-connected affiliative networks, with individuals less likely to interact in tightly knit cliques. Individuals in low predator pressure environments received more frequent agonsitic interactions, were more likely to initiate agonistic interactions with many members of their group and were more direct in their agonistic interactions, and these agonistic networks had more influential individuals.

Most affiliative social network measures were also correlated with relative rank. Specifically, affiliative indegree, outdegree, instrength, outstrength and eigenvector centrality were positively correlated with relative rank. Affiliative incloseness and outcloseness were negatively correlated with relative rank (Table A8). Many agonistic social network measures were also correlated with relative rank. Agonistic indegree, instrength, incloseness and eigenvector centrality were positively correlated with relative rank, while agonistic outdegree, outcloseness and betweenness were negatively correlated with relative rank (Table A9).

High-ranking individuals were also those individuals who were more involved with their affiliative social network. High-ranking individuals were also those who were more likely to interact frequently with more members of their group and were more influential in their affiliative network. Low-ranking individuals were also those who were more likely to have more direct affiliative interactions with others. Interestingly, high-ranking individuals were also those who were recipients of more frequent, direct agonistic interactions from more members of the group and were highly influential in their agonistic networks. Low-ranking individuals were also those who initiated more direct agonistic interactions against more members of their group and were more likely to interact with different social groups.

Fixed effects fitted on boldness

For fixed effects fitted on boldness (affiliative: Table A10, agonistic: Table A11), only alert distance had a negative, significant association with boldness in both affiliative and agonistic models, suggesting that bolder individuals were also those who allowed closer approach before alerting.

Fixed effects fitted on docility

For the fixed effects fitted on docility (affiliative: Table A12, agonistic: Table A13), relative rank was positively correlated with docility in all models, indicating that dominant individuals were also those who were more docile. The number of trapping events per year per colony was negatively correlated with docility in all models. This suggests trapping less often during the season influenced docility. Interestingly, age category (reference level: adult) was negatively correlated with agonistic indegree and outstrength. Thus, yearlings received agonistic interactions from more individuals in their social group and also initiated agonistic interactions more frequently. Sex (reference level: female) was positively correlated with agonistic outdegree, instrength, outstrength, incloseness and eigenvector centrality. Males initiated more frequent agonistic interactions with more individuals, received more frequent, direct agonistic interactions and were more influential in their social network.

Table A1
Ethogram of social behaviours of yellow-bellied marmots recorded during observations

Interaction	Category	Behaviour	Behavioural description
Aggression			
	Fight		Interactions happen quickly and are likely to be accompanied by vocalizations (squeaks, yelps, growls, etc.). Marmots separate quickly afterwards. There are eight types of fight behaviour
		Bite	Initiator aggressively bites receiver
		Box	Initiator stands on hindlegs and strikes opponent aggressively using its paws
		Chase	Initiator aggressively chases receiver
		Grab/slap/push	Initiator aggressively grabs, slaps or pushes receiver
		Mouth spar	Two marmots aggressively lunge at each other with open mouths
		Pounce	Initiator aggressively pounces on receiver
		Snap/snarl/hiss	Initiator aggressively vocalizes towards receiver
		Wrestle	Two marmots aggressively wrestle with each other
	Displacement		
		Simple displacement	Following contact between two marmots, one moves away
		Proximity displacement	Initiator marmot approaches another marmot within 1 m and the other marmot moves away
Affiliative			
	Play		Unlike aggression, play is 'bouncier' and individuals change roles repeatedly, regularly changing behaviours. Play can get interrupted, where individuals pause, look around or do other things that make them seem less invested. After a bout, they are likely to sit next to one another. There are eight play behaviours
		Bite	Initiator playfully bites receiver
		Box	Initiator stands on hindlegs and playfully strikes opponent with its paws
		Chase	Initiator playfully chases receiver
		Grab/slap/push	Initiator playfully grabs, slaps or pushes receiver
		Pounce	Initiator playfully pounces on receiver
		Mount	A mount in the context of play, where the initiator places its forepaws on another marmot's back and mounts it
		Wrestle	Initiator and receiver playfully wrestle with each other
		Greet	Initiator touches the nose of another marmot with its nose
	Sit		
		Sit <1 m	Marmots sit within 1 m of each other but make no body contact
		Sit body contact	Marmots sit in physical contact with each other
	Other		
		Follow	One marmot repeatedly approaches another and the approached animal moves away three or more times
		Forage together	Marmots forage within 1 m of each other or move together (less than 5 m apart)
		Allogroom	One marmot grooms another, or two or more marmots groom each other, often on areas of the body where individuals cannot groom themselves (back of neck)

Descriptions are written with a focus on the initiator individual. Adapted from Wey and Blumstein (2010).

Table A2
Results of bivariate models illustrating the among-individual variance of intercepts of the social network measure and boldness and the correlation at the individual level between boldness and the affiliative social network measure

Social network measure	V_{SNT}	$V_{boldness}$	Correlation
Indegree	0.480 (0.030/0.706)	0.0002 (<0.001/0.0009)	−0.259 (−0.856/0.719)
Outdegree	0.478 (0.292/0.682)	0.0002 (<0.0001/0.0009)	−0.069 (−0.829/0.725)
Instrength	0.442 (0.300/0.591)	0.0002 (<0.001/0.0009)	0.372 (−0.602/0.901)
Outstrength	0.420 (0.275/0.576)	0.0002 (<0.001/0.0009)	−0.133 (−0.896/0.615)
Incloseness	0.990 (0.673/1.35)	0.0002 (<0.001/0.0009)	0.214 (−0.636/0.900)
Outcloseness	0.955 (0.637/1.32)	0.0002 (<0.001/0.0009)	0.369 (−0.655/0.863)
Betweenness centrality	1.01 (0.675/1.41)	0.0002 (<0.001/0.0008)	−0.044 (−0.739/0.788)
Eigenvector centrality	0.901 (0.627/1.20)	0.0002 (<0.001/0.0009)	0.251 (−0.573/0.894)
Local clustering	0.619 (0.364/0.902)	0.0002 (<0.001/0.0009)	−0.085 (−0.801/0.745)

SNT: social network trait. We report the estimate with lower and upper 95% credible intervals in parentheses.

Table A3
Results of bivariate models illustrating the among-individual variance of intercepts of the social network measure and boldness and the correlation at the individual level between boldness and the agonistic social network measure

Social network measure	V_{SNT}	$V_{boldness}$	Correlation
Indegree	0.910 (0.614/1.22)	0.0002 (<0.0001/0.0009)	−0.059 (−0.744/0.779)
Outdegree	0.291 (0.174/0.421)	0.0002 (<0.0001/0.001)	−0.045 (−0.832/0.691)
Instrength	0.6754 (0.427/0.910)	0.0003 (<0.0001/0.001)	0.170 (−0.601/0.886)
Outstrength	0.276 (0.168/0.408)	0.0003 (<0.0001/0.001)	0.327 (−0.536/0.888)
Incloseness	0.892 (0.605/1.20)	0.0002 (<0.0001/0.001)	−0.061 (−0.767/0.770)
Outcloseness	0.522 (0.291/0.786)	0.0004 (<0.0001/0.001)	−0.552 (−0.966/0.387)
Betweenness centrality	0.640 (0.414/0.872)	0.0004 (<0.0001/0.001)	−0.557 (−0.938/0.406)
Eigenvector centrality	0.838 (0.540/1.19)	0.0003 (<0.0001/0.001)	0.478 (−0.562/0.924)
Local clustering	0.937 (0.637/1.27)	0.0004 (<0.0001/0.001)	0.615 (−0.323/0.971)

SNT: social network trait. We report the estimate with lower and upper 95% credible intervals in parentheses.

Table A4
Results of bivariate models illustrating the variance, covariance and correlation at the individual level between docility and the affiliative social network measure

Social network measure	V_{SNM}	$V_{docility}$	Correlation
Indegree	0.533 (0.437/0.634)	0.095 (0.064/0.126)	−0.166 (−0.355/0.014)
Outdegree	0.472 (0.380/0.554)	0.095 (0.065/0.126)	**−0.207 (−0.394/−0.026)**
Instrength	0.633 (0.525/0.747)	0.095 (0.065/0.127)	−0.084 (−0.290/0.060)
Outstrength	0.678 (0.561/0.797)	0.095 (0.066/0.129)	−0.094 (−0.283/0.069)
Incloseness	0.707 (0.579/0.833)	0.096 (0.066/0.127)	−0.054 (−0.247/0.109)
Outcloseness	0.955 (0.763/1.16)	0.099 (0.068/0.132)	**−0.208 (−0.407/−0.027)**
Betweenness centrality	1.02 (0.830/1.23)	0.096 (0.064/0.127)	−0.105 (−0.297/0.071)
Eigenvector centrality	0.781 (0.635/0.931)	0.096 (0.066/0.128)	**−0.182 (−0.359/−0.009)**
Local clustering	0.678 (0.545/0.829)	0.096 (0.066/0.128)	0.032 (−0.133/0.241)

SNM: social network measure. We report the estimate with lower and upper 95% credible intervals in parentheses. Bold results do not include zero in the credible interval.

Table A5
Results of bivariate models illustrating the variance, covariance and correlation at the individual level between docility and the agonistic social network measure

Social network measure	V_{SNM}	$V_{docility}$	Correlation
Indegree	0.661 (0.542/0.797)	0.077 (0.050/0.105)	−0.185 (−0.354/0.036)
Outdegree	0.627 (0.506/0.748)	0.077 (0.050/0.105)	**−0.149 (−0.397/−0.006)**
Instrength	0.708 (0.572/0.844)	0.078 (0.052/0.106)	**−0.214 (−0.406/−0.046)**
Outstrength	0.400 (0.323/0.482)	0.078 (0.050/0.105)	−0.116 (−0.280/0.060)
Incloseness	0.675 (0.549/0.801)	0.078 (0.052/0.106)	−0.169 (−0.362/0.047)
Outcloseness	0.702 (0.569/0.834)	0.078 (0.051/0.106)	**−0.218 (−0.412/−0.018)**
Betweenness centrality	1.09 (0.895/1.32)	0.078 (0.052/0.106)	−0.022 (−0.230/0.166)
Eigenvector centrality	0.666 (0.541/0.799)	0.077 (0.051/0.104)	**−0.195 (−0.361/−0.023)**
Local clustering	0.922 (0.745/1.03)	0.080 (0.053/0.110)	−0.092 (−0.306/0.069)

SNM: social network measure. We report the estimate with lower and upper 95% credible intervals in parentheses. Bold results do not include zero in the credible interval.

Table A6
Fixed effects fitted on social network measures for the bivariate models of affiliative social network measures and boldness

Social network measure	SNM: Intercept	Age category	Sex	Yearly predator index	Relative rank
Indegree	**1.59 (1.04/2.16)**	−0.125 (−0.366/0.112)	−0.073 (−0.418/0.280)	**0.709 (0.449/0.953)**	−0.077 (−0.520/0.418)
Outdegree	**1.28 (0.724/1.84)**	0.084 (−0.152/0.320)	0.129 (−0.214/0.502)	**0.704 (0.449/0.973)**	−0.270 (−0.775/0.247)
Instrength	**1.89 (1.39/2.37)**	**0.390 (0.237/0.538)**	0.017 (−0.298/0.334)	0.162 (−0.004/0.326)	−0.067 (−0.461/0.324)
Outstrength	**1.68 (1.17/2.16)**	**0.612 (0.437/0.790)**	0.208 (−0.102/0.536)	**0.272 (0.084/0.463)**	−0.489 (−0.478/0.358)
Incloseness	**0.870 (0.160/1.63)**	−0.141 (−0.360/0.080)	0.032 (−0.442/0.512)	**0.446 (0.210/0.686)**	0.126 (−0.454/0.752)
Outcloseness	**0.850 (0.107/1.57)**	**0.781 (0.524/1.03)**	−0.325 (−0.778/0.150)	**0.627 (0.359/0.910)**	**−0.768 (−1.39/−0.162)**
Betweenness centrality	−0.169 (−0.932/0.573)	**0.293 (0.032/0.565)**	−0.044 (−0.542/0.452)	**−0.809 (−1.10/−0.520)**	**−0.952 (−1.60/−0.303)**
Eigenvector centrality	0.384 (−0.302/1.06)	**0.365 (0.201/0.532)**	0.254 (−0.179/0.705)	0.178 (−0.115/0.352)	−0.077 (−0.575/0.432)
Local clustering	0.044 (−0.672/0.702)	0.096 (−0.241/0.410)	−0.321 (−0.780/0.103)	**0.468 (0.108/0.813)**	0.226 (−0.420/0.832)

SNM: social network measure. Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A7
Fixed effects fitted on social network measures within bivariate models of agonistic social network measures and boldness

Social network measure	SNM: Intercept	Age category	Sex	Yearly predator index	Relative rank
Indegree	0.102 (−0.602/0.792)	**−0.231 (−0.402/−0.047)**	−0.220 (−0.663/0.239)	**0.305 (0.097/0.517)**	**1.21 (0.589/1.76)**
Outdegree	**1.32 (0.892/1.79)**	**−1.09 (−1.31/−0.891)**	**0.418 (0.125/0.705)**	0.161 (−0.074/0.412)	−0.368 (−0.788/0.049)
Instrength	0.222 (−0.396/0.820)	**−0.823 (−1.04/−0.598)**	−0.009 (−0.416/0.376)	**0.371 (0.126/0.625)**	**1.38 (0.820/1.94)**
Outstrength	**0.529 (0.038/1.02)**	**−0.732 (−0.099/−0.461)**	**0.434 (0.105/0.749)**	0.209 (−0.108/0.493)	0.088 (−0.395/0.539)
Incloseness	**1.25 (0.029/1.51)**	**−0.218 (−0.423/−0.017)**	−0.207 (−0.675/0.253)	−0.050 (−0.299/0.190)	0.447 (−0.151/1.02)
Outcloseness	**1.55 (0.960/2.21)**	**−0.761 (−1.06/−0.456)**	−0.017 (−0.438/0.374)	−0.250 (−0.582/0.080)	−0.215 (−0.780/0.347)
Betweenness centrality	0.351 (−0.284/0.946)	**−0.608 (−0.818/−0.381)**	0.126 (−0.286/0.517)	0.102 (−0.156/0.369)	0.317 (−0.248/0.843)
Eigenvector centrality	0.068 (−0.605/0.798)	−0.045 (−0.310/0.217)	0.116 (−0.367/0.564)	**0.353 (0.047/0.668)**	**−0.923 (−1.54/−0.252)**
Local clustering	−0.412 (−1.12/0.288)	0.007 (−0.157/0.192)	−0.224 (−0.714/0.226)	0.041 (−0.168/0.252)	0.471 (−0.090/1.03)

SNM: social network measure. Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A8
Fixed effects fitted on social network measures for the bivariate models of affiliative social network measures and docility

Social network measure	SNM: Intercept	Age category	Sex	Yearly predator index	Relative rank
Indegree	**1.89 (1.49/2.30)**	**0.304 (0.250/0.357)**	−0.122 (−0.307/0.050)	**0.245 (0.185/0.304)**	**0.459 (0.346/0.579)**
Outdegree	**1.77 (1.37/2.17)**	**0.265 (0.205/0.323)**	0.173 (−0.006/0.341)	**0.209 (0.139/0.271)**	**0.233 (0.109/0.363)**
Instrength	**2.54 (2.11/2.99)**	**0.244 (0.196/0.291)**	−0.040 (−0.230/0.150)	−0.009 (−0.063/0.0427)	**0.191 (0.091/0.300)**
Outstrength	**2.58 (2.11/3.03)**	**0.132 (0.088/0.177)**	**0.304 (0.107/0.508)**	0.024 (−0.024/0.740)	**0.212 (0.116/0.313)**
Incloseness	**0.946 (0.462/1.42)**	**0.157 (0.098/0.216)**	−0.008 (−0.211/0.195)	**0.719 (0.652/0.787)**	**−0.281 (−0.411/−0.147)**
Outcloseness	**0.629 (0.100/1.18)**	**0.320 (0.251/0.391)**	−0.078 (−0.319/0.165)	**1.04 (0.966/1.12)**	**−0.356 (−0.508/−0.208)**
Betweenness centrality	**0.577 (−0.003/1.16)**	**−0.389 (−0.479/−0.296)**	−0.065 (−0.329/0.179)	−0.072 (−0.173/0.025)	0.079 (−0.113/0.272)
Eigenvector centrality	−0.047 (−0.549/0.471)	**0.640 (0.567/0.713)**	0.149 (−0.072/0.367)	−0.019 (−0.096/0.067)	**0.786 (0.630/0.953)**
Local clustering	−0.408 (−0.924/0.065)	**0.263 (0.161/0.365)**	−0.098 (−0.319/0.107)	**−0.460 (0.347/0.575)**	−0.807 (−0.219/0.204)

SNM: social network measure. Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A9
Fixed effects fitted on social network measures for the bivariate models of agonistic social network measures and docility

Social network measure	SNM: Intercept	Age category	Sex	Yearly predator index	Relative rank
Indegree	**0.710 (0.247/1.18)**	**−0.084 (−0.148/−0.016)**	−0.051 (−0.262/0.152)	0.072 (−0.003/0.150)	**0.235 (0.082/0.375)**
Outdegree	**2.16 (1.73/2.62)**	**−0.725 (−0.787/−0.666)**	**0.291 (0.085/0.497)**	**0.188 (0.117/0.253)**	**−0.450 (−0.579/−0.316)**
Instrength	**0.504 (0.028/0.982)**	**−0.299 (−0.368/−0.231)**	−0.068 (−0.282/0.151)	**0.090 (0.013/0.170)**	**0.956 (0.803/1.11)**
Outstrength	**0.939 (0.550/1.31)**	**−0.601 (−0.688/−0.521)**	**0.319 (0.145/0.492)**	0.093 (−0.005/0.184)	−0.641 (−0.233/0.112)
Incloseness	**1.47 (0.995/1.92)**	**−0.222 (−0.276/−0.169)**	0.082 (−0.128/0.293)	**0.127 (0.066/0.185)**	**0.817 (0.699/0.934)**
Outcloseness	**2.39 (1.92/2.85)**	**−0.393 (−0.456/−0.332)**	−0.065 (−0.281/0.151)	**0.159 (0.088/0.227)**	**−0.152 (−0.283/−0.013)**
Betweenness centrality	**1.06 (0.463/1.65)**	**−0.208 (−0.288/−0.128)**	0.031 (−0.218/0.317)	−0.080 (−0.168/0.016)	**−0.380 (−0.553/−0.201)**
Eigenvector centrality	**0.249 (−0.245/0.703)**	**−0.398 (−0.475/−0.320)**	0.034 (−0.186/0.247)	−0.017 (−0.106/0.073)	**0.609 (0.449/0.779)**
Local clustering	−0.407 (−0.966/0.134)	**0.412 (0.328/0.492)**	−0.029 (−0.268/0.224)	**0.157 (0.063/0.249)**	0.088 (−0.091/0.267)

SNM: social network measure. Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A10
Fixed effects fitted on boldness for the bivariate models of affiliative social network measures and boldness

Social network measure	Boldness: Intercept	Age category	Sex	Yearly predator index	Relative rank	Days since last event	Events per year per colony	Time of day (morning/afternoon)
Indegree	**0.121 (0.048/0.199)**	0.0005 (-0.035/0.039)	0.013 (-0.018/0.044)	-0.009 (-0.059/0.040)	-0.002 (-0.052/0.042)	-0.0008 (-0.002/0.0005)	0.0008 (-0.0007/0.002)	0.0004 (-0.026/0.027)
Outdegree	**0.122 (0.048/0.200)**	0.0002 (-0.037/0.036)	0.013 (-0.018/0.043)	-0.009 (-0.059/0.038)	-0.002 (-0.049/0.046)	-0.0008 (-0.002/0.0007)	0.0008 (-0.0007/0.002)	0.0002 (-0.026/0.026)
Instrength	**0.125 (0.047/0.204)**	0.0008 (-0.036/0.038)	0.013 (-0.017/0.044)	-0.007 (-0.057/0.043)	-0.003 (-0.051/0.044)	-0.0009 (-0.002/0.0007)	0.0007 (-0.0008/0.002)	0.0003 (-0.029/0.024)
Outstrength	**0.119 (0.045/0.201)**	-0.001 (-0.040/0.034)	0.013 (-0.018/0.043)	-0.009 (-0.058/0.041)	-0.0004 (-0.046/0.049)	-0.0006 (-0.002/0.0006)	0.0008 (-0.0007/0.002)	<0.0001 (-0.026/0.027)
Incloseness	**0.122 (0.046/0.198)**	-0.001 (-0.038/0.035)	0.013 (-0.018/0.044)	-0.008 (-0.055/0.043)	-0.002 (-0.048/0.046)	-0.0008 (-0.002/0.0007)	0.0008 (-0.0007/0.002)	-0.0005 (-0.026/0.026)
Outcloseness	**0.122 (0.047/0.203)**	0.0005 (-0.037/0.037)	0.013 (-0.017/0.044)	-0.008 (-0.059/0.041)	-0.003 (-0.052/0.045)	-0.0008 (-0.002/0.0006)	0.0008 (-0.0006/0.002)	-0.0005 (-0.026/0.026)
Betweenness centrality	**0.121 (0.045/0.196)**	0.0001 (-0.036/0.036)	0.013 (-0.016/0.043)	-0.009 (-0.058/0.040)	-0.002 (-0.049/0.044)	-0.0008 (-0.002/0.0006)	0.0008 (-0.0006/0.002)	-0.0003 (-0.026/0.027)
Eigenvector centrality	**0.120 (0.045/0.196)**	0.0001 (-0.037/0.035)	0.012 (-0.019/0.043)	-0.007 (-0.055/0.043)	-0.003 (-0.051/0.045)	-0.0008 (-0.002/0.0006)	0.0008 (-0.0008/0.002)	<-0.0001 (-0.027/0.026)
Local clustering	**0.121 (0.044/0.198)**	-0.0003 (-0.036/0.037)	0.013 (-0.018/0.041)	-0.008 (-0.057/0.041)	-0.002 (-0.048/0.046)	-0.0008 (-0.002/0.0006)	0.0008 (-0.0007/0.002)	<0.0001 (-0.026/0.026)
	Alert distance	**Burrow distance**						
Indegree	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)						
Outdegree	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0008)						
Instrength	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0009)						
Outstrength	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0007)						
Incloseness	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0009)						
Outcloseness	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)						
Betweenness centrality	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)						
Eigenvector centrality	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0009)						
Local clustering	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)						

Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A11
Fixed effects fitted on boldness within bivariate models of agonistic social network measures and boldness

Social network measure	Boldness: Intercept	Age category	Sex	Yearly predator index	Relative rank	Days since last event	Events per year per colony	Time of day (morning/afternoon)
Indegree	**0.121 (0.036/0.205)**	-0.004 (-0.043/0.036)	0.011 (-0.022/0.043)	-0.001 (-0.058/0.057)	0.003 (-0.047/0.049)	-0.0008 (-0.002/0.0008)	0.0008 (-0.0008/0.002)	0.004 (-0.027/0.030)
Outdegree	**0.123 (0.040/0.208)**	-0.004 (-0.045/0.035)	0.011 (-0.020/0.044)	-0.0009 (-0.055/0.057)	0.003 (-0.044/0.052)	-0.0009 (-0.002/0.0007)	0.0007 (-0.0008/0.002)	0.00002 (-0.028/0.028)
Instrength	**0.124 (0.040/0.206)**	-0.005 (-0.047/0.033)	0.011 (-0.022/0.044)	-0.0002 (-0.057/0.059)	0.004 (-0.046/0.053)	-0.0009 (-0.003/0.0007)	0.0007 (-0.0008/0.002)	0.0003 (-0.027/0.028)
Outstrength	**0.123 (0.040/0.206)**	-0.001 (-0.04/0.039)	0.009 (-0.023/0.043)	0.00008 (-0.055/0.056)	0.003 (-0.045/0.051)	-0.0009 (-0.002/0.0007)	0.0007 (-0.0009/0.002)	0.0002 (-0.029/0.027)
Incloseness	**0.122 (0.044/0.210)**	-0.004 (-0.047/0.034)	0.010 (-0.022/0.043)	-0.0007 (-0.058/0.055)	0.0029 (-0.046/0.051)	-0.0009 (-0.002/0.0006)	0.0008 (-0.0009/0.002)	0.0003 (-0.028/0.028)
Outcloseness	**0.122 (0.039/0.201)**	0.002 (-0.004/0.005)	0.0009 (-0.002/0.004)	-0.001 (-0.005/0.006)	-0.0004 (-0.053/0.050)	-0.0009 (-0.002/0.0007)	0.0006 (-0.001/0.002)	0.00001 (-0.027/0.028)
Betweenness centrality	**0.131 (0.047/0.216)**	-0.0006 (-0.039/0.041)	0.011 (-0.021/0.044)	-0.0005 (-0.053/0.057)	0.001 (-0.048/0.050)	-0.0009 (-0.002/0.0007)	0.0005 (-0.001/0.002)	0.0002 (-0.027/0.029)
Eigenvector centrality	**0.117 (0.030/0.199)**	-0.003 (-0.043/0.037)	0.010 (-0.023/0.041)	-0.0002 (-0.059/0.055)	0.001 (-0.049/0.050)	-0.0009 (-0.003/0.0007)	0.0009 (-0.0007/0.003)	0.0003 (-0.026/0.030)
Local clustering	**0.122 (0.042/0.207)**	-0.007 (-0.047/0.034)	0.011 (-0.022/0.044)	-0.001 (-0.056/0.056)	0.003 (-0.047/0.052)	-0.0008 (-0.002/0.0008)	0.0007 (-0.0009/0.002)	-0.0003 (-0.028/0.027)
	Alert distance	**Burrow distance**						
Indegree	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0009)						
Outdegree	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0009)						
Instrength	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0008)						
Outstrength	**-0.0008(-0.001/-0.0003)**	-0.0005(-0.002/0.0008)						
Incloseness	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0008)						
Outcloseness	**-0.0008(-0.001/-0.0002)**	-0.0006(-0.002/0.0007)						
Betweenness centrality	**-0.0008(-0.001/-0.0003)**	-0.0006(-0.002/0.0008)						
Eigenvector centrality	**-0.0008(-0.001/-0.0002)**	-0.0005(-0.002/0.0009)						
Local clustering	**-0.0008(-0.001/-0.0002)**	-0.0004(-0.002/0.0009)						

Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.

Table A12
Fixed effects fitted on docility within bivariate models of affiliative social network measures and docility

| Social network measure	Docility: Intercept	Age category	Sex	Yearly predator index	Relative rank	Days since last event	Events per year per colony	Time of day (morning/afternoon)
Indegree	**0.515 (0.265/0.778)**	−0.042 (−0.129/0.049)	0.084 (−0.018/0.186)	0.035 (−0.066/0.143)	**0.215 (0.077/0.363)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0002)**	0.037 (−0.022/0.092)
Outdegree	**0.513 (0.258/0.768)**	−0.042 (−0.131/0.042)	0.086 (−0.014/0.187)	0.041 (−0.065/0.145)	**0.218 (0.079/0.363)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0002)**	0.037 (−0.020/0.093)
Instrength	**0.511 (0.252/0.777)**	−0.053 (−0.137/0.034)	0.083 (−0.022/0.183)	0.025 (−0.082/0.132)	**0.244 (0.100/0.389)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0001)**	0.037 (−0.019/0.010)
Outstrength	**0.512 (0.245/0.762)**	−0.051 (−0.142/0.031)	0.084 (−0.024/0.184)	0.026 (0.077/0.133)	**0.239 (0.098/0.380)**	0.001 (−0.001/0.003)	**<−0.001 (−0.002/<−0.001)**	0.038 (−0.017/0.097)
Incloseness	**0.510 (0.240/0.764)**	−0.053 (−0.137/0.034)	0.084 (−0.016/0.191)	0.030 (−0.075/0.138)	**0.243 (0.102/0.388)**	0.001 (−0.001/0.003)	<−0.001 (−0.002/<0.001)	0.039 (−0.017/0.096)
Outcloseness	**0.510 (0.251/0.776)**	−0.056 (−0.143/0.029)	0.079 (−0.019/0.189)	0.016 (−0.091/0.123)	**0.251 (0.108/0.395)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0002)**	0.039 (−0.017/0.097)
Betweenness centrality	**0.513 (0.258/0.775)**	−0.047 (−0.135/0.037)	0.084 (−0.022/0.186)	0.032 (−0.074/ 0.138)	**0.234 (0.091/0.373)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0001)**	0.037 (−0.019/0.096)
Eigenvector centrality	**0.535 (0.277/0.790)**	−0.044 (−0.130/ 0.043)	0.085 (−0.018/0.189)	0.030 (−0.076/0.133)	**0.201 (0.054/0.346)**	0.001 (−0.001/0.003)	**−0.001 (−0.002/−0.0001)**	0.037 (−0.018/0.094)
Local clustering	**0.513 (0.254/0.774)**	−0.052 (−0.138/0.034)	0.083 (−0.021/0.186)	0.032 (−0.071/0.144)	**0.239 (0.098/0.383)**	0.001 (−0.001/0.003)	**<−0.001 (−0.002/<−0.001)**	0.037 (−0.019/0.095)

Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals between parentheses. Bold values had credible intervals that did not include zero.

Table A13
Fixed effects fitted on docility for the bivariate models of agonistic social network measures and docility

Social network measure	Docility: Intercept	Age category	Sex	Yearly predator index	Relative rank	Days since last event	Events per year per colony	Time of day (morning/afternoon)
Indegree	**0.710 (0.247/1.18)**	**−0.084 (−0.148/−0.016)**	−0.051 (−0.262/0.152)	−0.005 (−0.119/0.098)	**0.235 (0.082/0.375)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.028 (−0.030/0.089)
Outdegree	**0.571 (0.315/0.832)**	−0.087 (−0.177/0.001)	**0.112 (0.014/0.222)**	0.002 (−0.111/0.117)	**0.266 (0.125/0.411)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.028 (−0.032/0.087)
Instrength	**0.556 (0.295/0.814)**	−0.074 (−0.164/0.016)	**0.106 (0.005/0.208)**	−0.010 (−0.126/0.103)	**0.234 (0.090/0.377)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.027 (−0.033/0.087)
Outstrength	**0.574 (0.296/0.826)**	**−0.094 (−0.187/−0.003)**	**0.114 (0.011/0.217)**	<−0.001 (−0.111/0.119)	**0.259 (0.114/0.403)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.028 (−0.031/0.089)
Incloseness	**0.583 (0.330/0.845)**	−0.077 (−0.170/0.001)	**0.109 (0.005/0.213)**	−0.103 (−0.129/0.105)	**0.235 (0.089/0.381)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/−0.001)**	0.028 (−0.032/0.087)
Outcloseness	**0.566 (0.307/0.825)**	−0.079 (−0.170/0.014)	0.109 (0.005/0.216)	−0.005 (−0.123/0.105)	**0.259 (0.112/0.405)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.028 (−0.036/0.086)
Betweenness centrality	**0.581 (0.314/0.838)**	−0.090 (−0.181/0.019)	0.113 (0.008/0.215)	0.002 (−0.113/0.122)	**0.260 (0.119/0.411)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.029 (−0.030/0.090)
Eigenvector centrality	**0.595 (0.328/0.846)**	−0.087 (−0.179/0.003)	**0.113 (0.011/0.219)**	0.004 (−0.110/0.121)	**0.239 (0.084/0.376)**	0.001 (−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.028 (−0.032/0.089)
Local clustering	**0.576 (0.314/0.845)**	−0.092 (−0.182/0.0009)	0.111 (0.004/0.212)	−0.006 (−0.125/0.107)	**0.260(0.120/0.412)**	0.001 (<−0.001/0.004)	**−0.001 (−0.002/<−0.001)**	0.029 (−0.030/0.091)

Adult was the reference level for age category. Female was the reference level for sex. We report estimate with lower and upper 95% credible intervals in parentheses. Bold values had credible intervals that did not include zero.
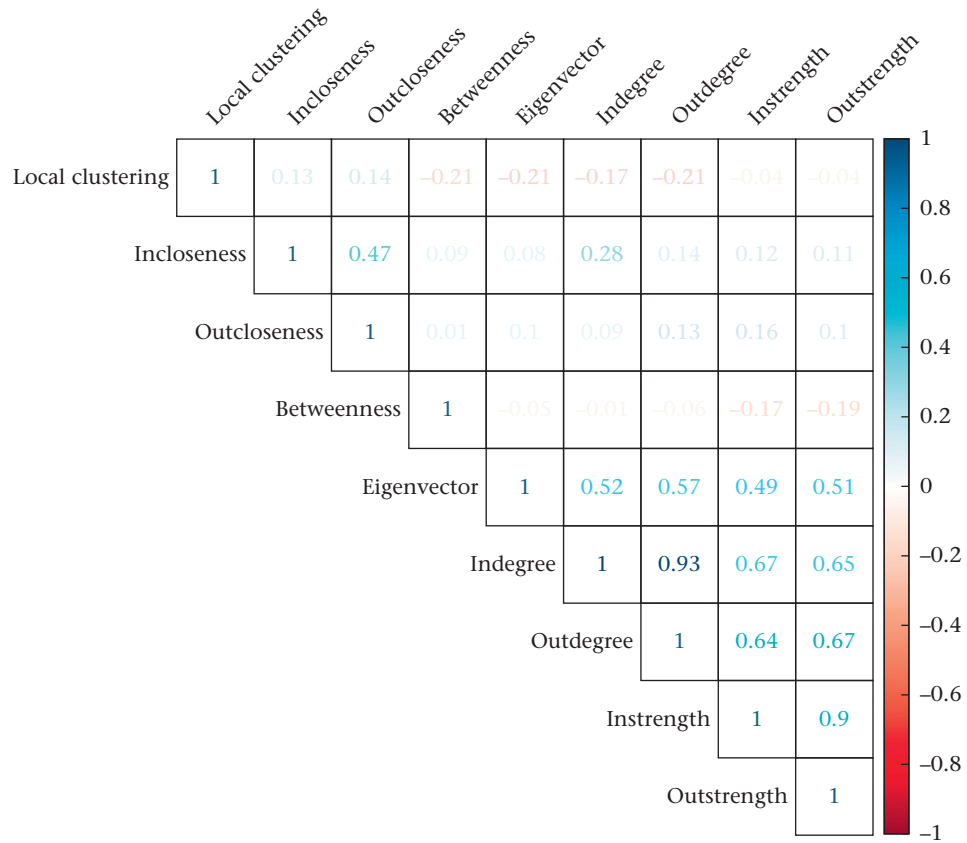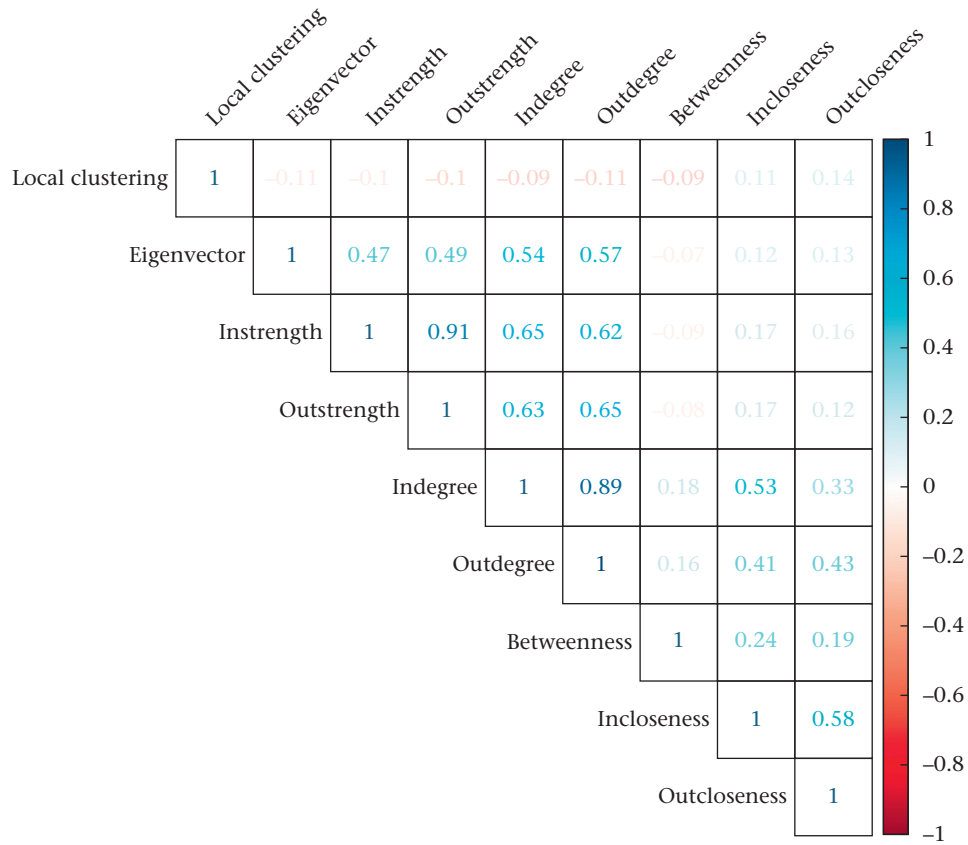
Figure A1. Correlations between social network measures in the affiliative–boldness data set. Correlations were calculated with Pearson's method and included all complete pairwise observations. Dark colours represent stronger correlations and light colours represent weaker correlations. Blue indicates the correlation is positive, red indicates the correlation is negative.
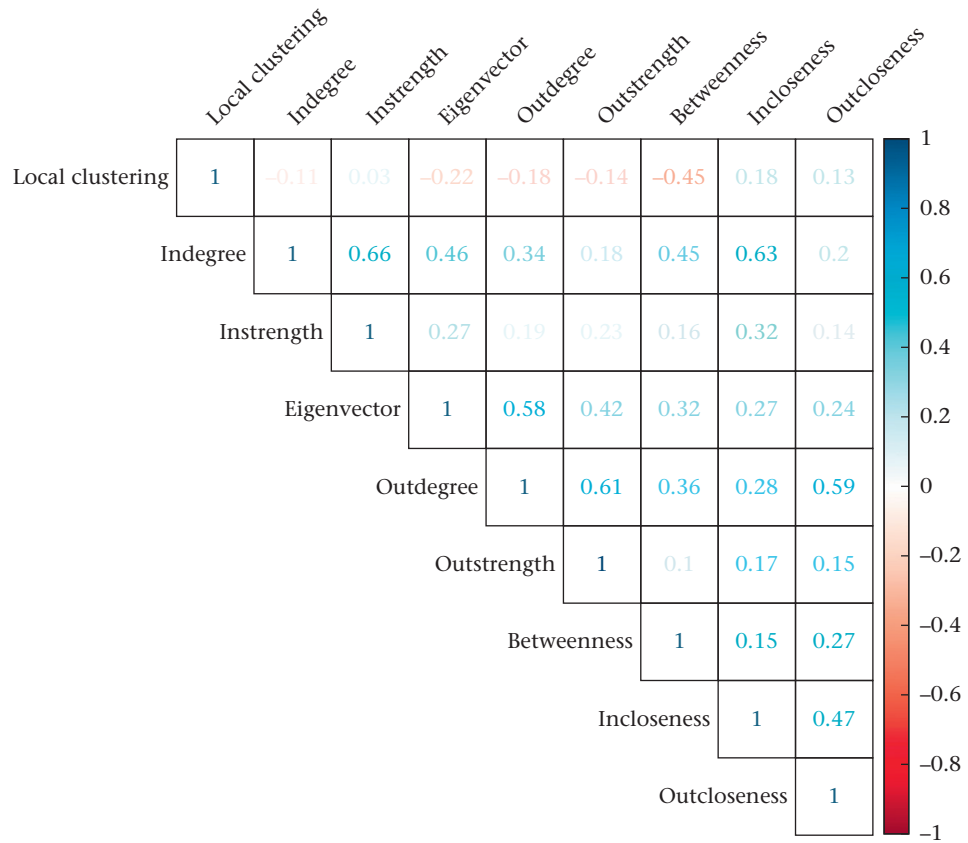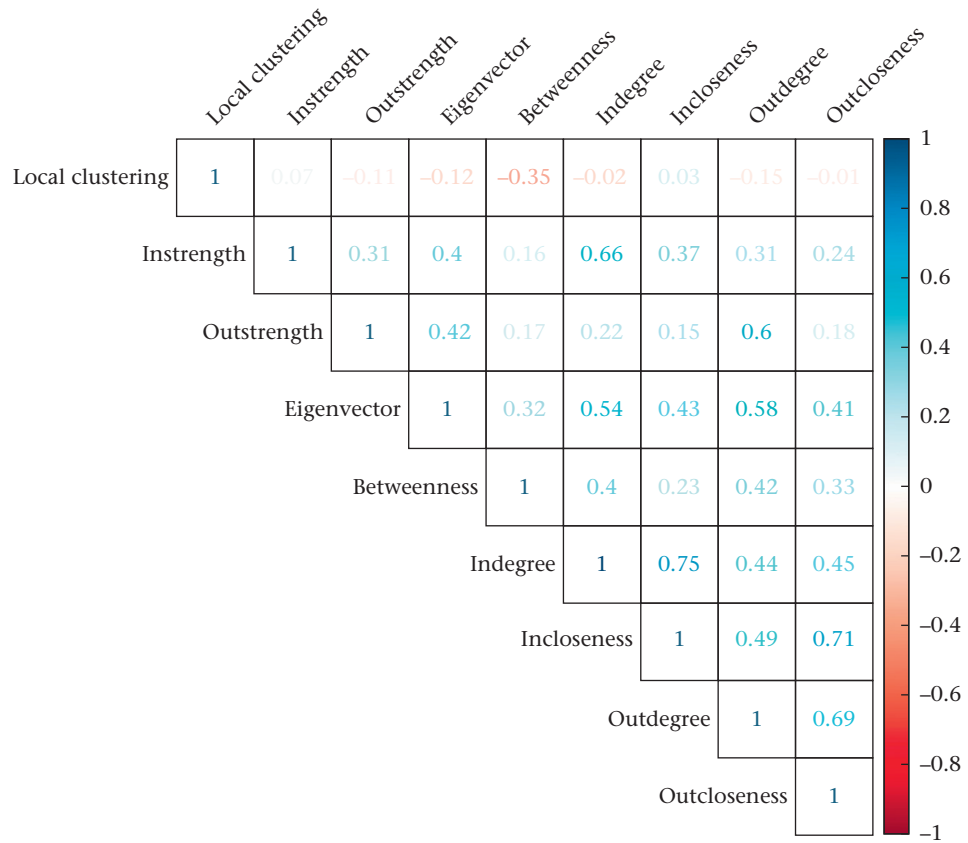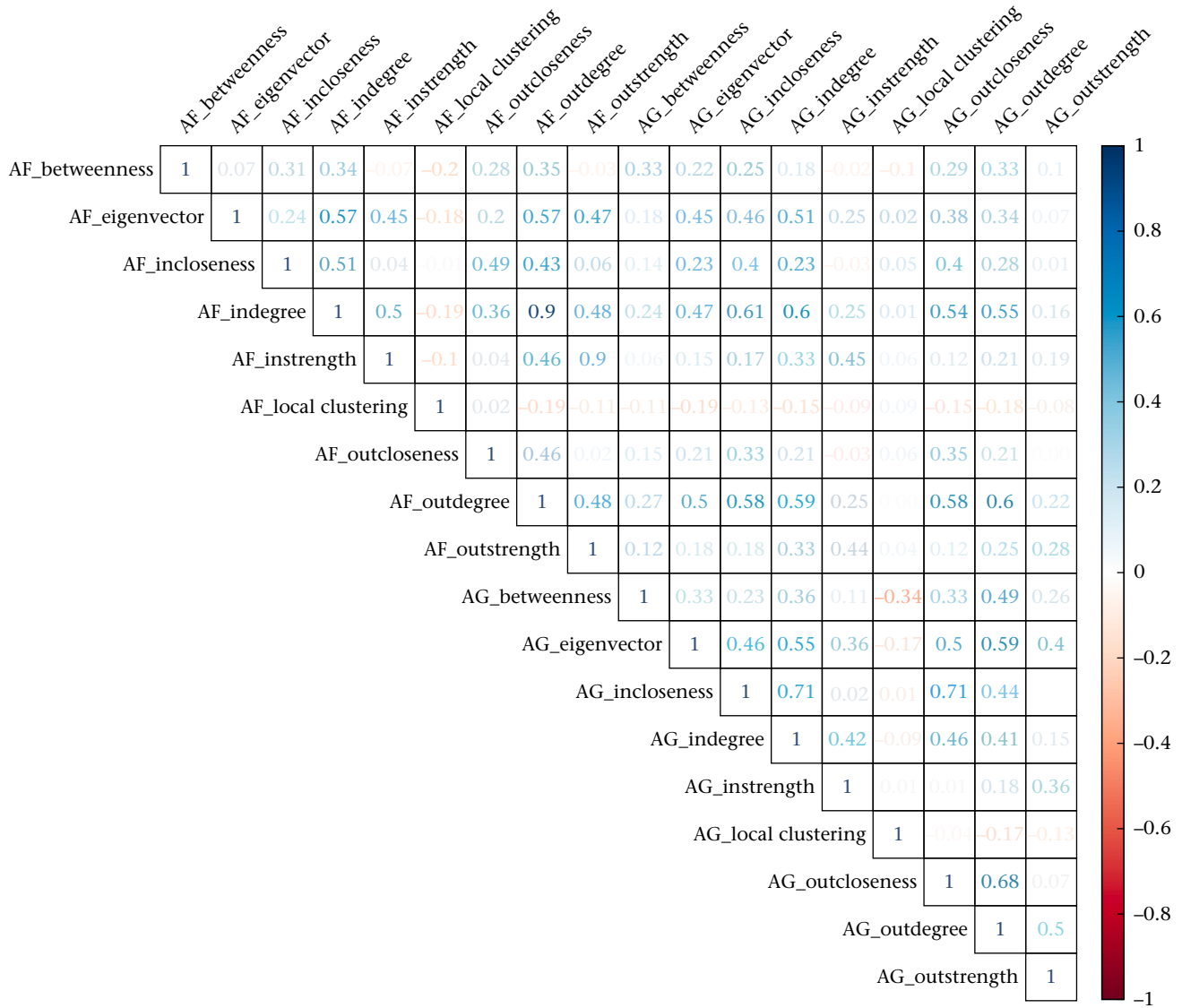
Figure A2. Correlations between social network measures in the agonistic–boldness data set. Correlations were calculated with Pearson's method and included all complete pairwise observations. Dark colours represent stronger correlations and light colours represent weaker correlations. Blue indicates the correlation is positive, red indicates the correlation is negative.

Figure A3. Correlations between social network measures in the affiliative—docility data set. Correlations were calculated with Pearson's method and included all complete pairwise observations. Dark colours represent stronger correlations and light colours represent weaker correlations. Blue indicates the correlation is positive, red indicates the correlation is negative.

Figure A4. Correlations between social network measures in the agonistic−docility data set. Correlations were calculated with Pearson's method and included all complete pairwise observations. Dark colours represent stronger correlations and light colours represent weaker correlations. Blue indicates the correlation is positive, red indicates the correlation is negative.

Figure A5. Correlations between social network measures in a combined agonistic–affiliative (AG–AF) data set. Correlations were calculated with Pearson's method and included all complete pairwise observations. Dark colours represent stronger correlations and light colours represent weaker correlations. Blue indicates the correlation is positive, red indicates the correlation is negative.