

## Research



**Cite this article:** Cook PA, Baker OM, Costello RA, Formica VA, Brodie III ED. 2022 Group composition of individual personalities alters social network structure in experimental populations of forked fungus beetles. *Biol. Lett.* **18**: 20210509.  
<https://doi.org/10.1098/rsbl.2021.0509>

Received: 24 September 2021  
Accepted: 24 February 2022

**Subject Areas:**  
behaviour

**Keywords:**  
animal personality, group composition, social networks, forked fungus beetles

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5880023>.

## Animal behaviour

# Group composition of individual personalities alters social network structure in experimental populations of forked fungus beetles

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Social network structure is a critical group character that mediates the flow of information, pathogens and resources among individuals in a population, yet little is known about what shapes social structures. In this study, we experimentally tested whether social network structure depends on the personalities of individual group members. Replicate groups of forked fungus beetles (*Bolitotherus cornutus*) were engineered to include only members previously assessed as either more social or less social. We found that individuals expressed consistent personalities across social contexts, exhibiting repeatable numbers of interactions and numbers of partners. Groups composed of more social individuals formed networks with higher interaction rates, higher tie density, higher global clustering and shorter average shortest paths than those composed of less social individuals. We highlight group composition of personalities as a source of variance in group traits and a potential mechanism by which networks could evolve.

## 1. Introduction

Animal social networks describe patterns of interaction among individuals. The position an individual occupies within a network modulates its exposure to information, parasites, pathogens, grooming and other consequences of sociality [1–7]. Over the last two decades, research across a range of taxa has confirmed that individual social network position has fitness consequences [8–20]. Position within a network is known to be a repeatable trait both within the same group [21–25] and in some species across social contexts [26–28]. Revealing the sources of variation in individual network position has led to a deeper understanding of how and when such traits are expected to evolve [29,30].

Much less is known about the causes and consequences of variation in network structure at the group level [31]. Group social network structures are emergent traits generated by the interactions of all group members. These structures affect ecological processes such as the transmission of information and disease, as well as a number of other demographic and evolutionary phenomena (reviewed in [30,32,33]). It is often suggested that network structure can be adaptive [29,34–36], although only a few studies have demonstrated this empirically [13,15,37–40]. Network structures are repeatable across years or environments in some species [26,41–45], adding further evidence that they are non-random.

One possible source of variation in network structures is the composition of individual personalities within groups. If individuals differ and maintain these differences across social contexts, group-level traits may depend on the

composition of the group. Behavioural types of group members are known to affect other emergent traits, including group activity [46], foraging success [47,48], prey capture [49,50], mating system [51], and collective offspring care [52]. There is evidence that group composition is a source of variation in social network structure (reviewed in [30]), but this work has focused on traits that can be phenotyped in isolation [53,54].

No studies have investigated how shifting the frequencies of social personalities within a group impacts network structure, despite growing interest in sociality as a personality trait [55]. The inherently multi-level nature of networks creates a clear link between individual behaviour and overall structure—a group whose members interact frequently and widely must have a densely connected network, while a group whose members interact rarely with few partners will have a sparse network. What is not known is whether individual behavioural types are consistent properties of individuals maintained in new social contexts, such that altering their frequencies will create variation in networks [56]. Alternatively, if individuals alter their behaviour to fill social niches [57,58], network structure may effectively be regulated and will not differ with group composition. In other words, we are asking whether individual behaviour is a predictor of social structures or solely an outcome of them. Insight into how group traits arise and how they can change requires understanding how the traits of individuals affect the group as a whole.

We experimentally manipulated replicate populations of the forked fungus beetle *Bolitotherus cornutus* to test whether individuals have repeatable social personalities and whether changing the distribution of these social personalities within a group alters network structure. Using the power of replicate experimental networks [56,59], we were able to control the environmental and demographic variables that have hindered past inference about group differences [60], engineering populations that differed only in the social tendencies of their members. We assayed the level of sociality of each individual in initial populations and then created experimental populations composed of either highly social or less social individuals. This approach allowed us to ask whether variation in social behaviour is a personality trait maintained in a new context and how it affects the overall architecture of interactions.

## 2. Material and methods

### (a) Study system

*Bolitotherus cornutus* is a tenebrionid beetle found on bracket fungi on rotting logs in the forests of eastern North America. Beetles within a forest are structured into subpopulations consisting of beetles living on a single log, where adults feed, interact and oviposit on the fungus [61,62]. Social interactions are easily observed on the surface of the log and brackets. Past work has found that multiple metrics of social network position are repeatably expressed by *B. cornutus* over a few weeks, even after disturbance, when individuals remain in the same social groups [63]. These metrics of individual position in non-mating networks are under strong but variable selection [19,64]. Group-level network traits are also under selection in this species; a recent multi-level selection study found that females have lower reproductive success in populations with higher social tie density [40].

### (b) Experimental design

We built 10 large screen enclosures (electronic supplementary material, figure S1A) in the forest around Mountain Lake Biological Station (37°22'37.0" N, 80°31'17.5" W), each containing a shelf holding 18 bags of hardwood sawdust inoculated with a laboratory-grown strain of the *B. cornutus* host fungus *Ganoderma tsugae*. The shelves served as artificial logs, studded with clumps of fungus brackets of the same size and genotype (electronic supplementary material, figure S1B).

We created 10 initial populations of 30 adult *B. cornutus* (electronic supplementary material, figure S1C) to be placed into the enclosures in June of 2019. These beetles had been held in isolation for a month prior. All individuals were identifiable by unique three-character codes printed on florescent paper and attached to their elytra with a UV-cured acrylic glue (Tuffleye Wet-A-Hook Technologies, San Antonio, TX). We measured the body size of each beetle from an image taken on a flatbed scanner (Epson Perfection V600 Photo) using ImageJ [65]. We then assembled 10 populations of 15 males and 15 females each that did not differ in average body size ( $F_{9,289} = 0.06$ ,  $p = 1$ ). Individuals were placed onto the artificial log haphazardly and allowed to acclimatize to their new environment for 36 h before behavioural observation.

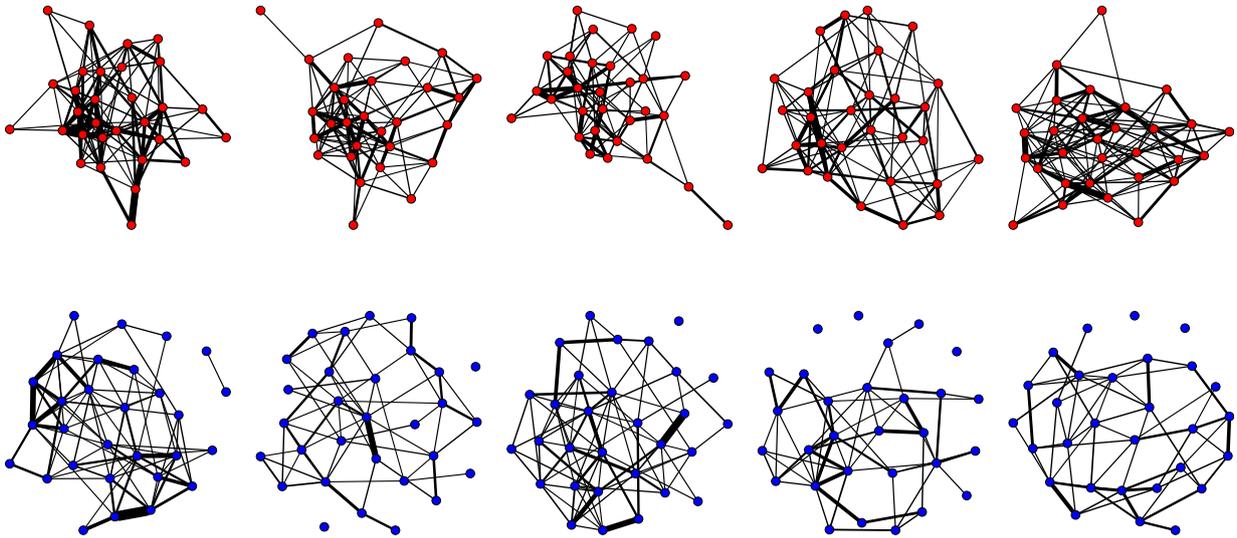
We phenotyped each individual's level of sociality in the initial populations. Our study system allows us to perform scan sampling of dyadic interactions, which is preferable for animal network studies because it maximizes the number of edges that can be observed and increases the robustness of the network to sampling biases [66–68]. We surveyed all visible beetles three times a day for 8 days. Social interactions were defined as individuals being in close proximity (within 5 cm) to one another [64]. The total number of interactions observed over the 24 surveys was tallied for each beetle as a measure of sociality. We then collected all beetles and held them in isolation for 5 days, which is sufficient time for social networks to 'reset' [63].

We reassigned individuals to new experimental populations on the basis of their observed number of social interactions, creating five populations of previously highly social beetles (mean prior interactions = 10, s.d. = 3) and five of previously less social beetles (mean prior interactions = 4, s.d. = 2; electronic supplementary material, figure S3). Population assignment was controlled so that mean body size did not differ among populations ( $F_{9,287} = 1.19$ ,  $p = 0.30$ ) and the number of beetles placed together that had previously interacted was minimized. After 36 h, we surveyed social interactions for 8 days using the exact methods described above. See electronic supplementary material for additional details on experimental design and surveying.

Beetles that died during the experiment ( $N = 4$ ) were removed from the networks. Observations of individuals that could not confidently be identified were excluded, but interactions with these individuals were still counted in their partner's social phenotypes. Our dataset consists of 10 initial networks (comprised 1041 interactions among 297 beetles; electronic supplementary materials, figure S2) and 10 experimental networks (1341 interactions among 296 beetles; figure 1).

### (c) Statistical analysis

We first asked whether two measures of sociality, number of interactions and number of partners, were repeatable from the initial social environment to the experimentally manipulated context. Repeatability is measured as the proportion of trait variance attributable to differences among individuals [69]. Gaussian linear mixed models with one random effect, individual identity [70], were run in the R package MCMCglmm [71,72] with uninformative priors for all parameters for 500 000 iterations, discarding the first 5000 as burn-in and using a thinning interval of 100. Variable traces were stationary and did not display autocorrelation, and chains



**Figure 1.** Networks from the 10 experimental populations. Networks composed of highly social individuals (red points) differ in number, thickness and distribution of ties from those networks composed of less social individuals (blue points). Line thickness is proportional to the simple ratio index, and nodes are plotted using an algorithm that places tightly connected pairs close together.

converged well (Gelman-Rubin criterion = 1 for all models). We extracted the among-individual variance component and divided it by the sum of among- and within- individual variance [70,73], reporting the kernel density estimate of repeatability. We then compared the observed value to those calculated from 1000 permuted datasets in which the identities of nodes in the second half of the experiment were randomized. Permutation tests are used to account for sampling biases and nuisance effects in network analyses [74], although we note that they may not fully account for issues of non-independence in interaction data [75]. To assess whether the results were due to confounding effects of treatment, we performed one permutation test shuffling only within treatments and another shuffling across treatments.

We then asked whether social network structures differed based on population composition. We constructed 20 undirected, weighted social networks using the simple ratio index, which quantifies the strength of interaction between each dyad from 0 to 1 [76]. Our 24 observation periods were sufficient to estimate variance in how often dyads interact with high precision [77]. We compared four group-level network metrics between treatments: interaction rate, tie density, global clustering coefficient and length of the average shortest path between pairs. These four metrics capture different aspects of how ‘connected’ networks are. They, respectively, quantify how many interactions occur per day, how many of the possible pairs are connected, how many of the possible triads are closed, and how closely linked any given pair is. Network-level metrics can be compared with conventional statistical methods when the networks are of equal size and sampled with the same methods [74,78,79]; see the electronic supplementary material for further details on how our design minimized differences among replicates. We used one-sided t-tests to test whether the populations of previously more social beetles had more interactions, higher tie density, higher clustering and lower average shortest path lengths, as we would expect if these individuals remained highly social. All analyses were performed in R v. 4.0.2 [80]. Weighted clustering and shortest path lengths were calculated in tnet [81], using the arithmetic mean weighting method for clustering [82], and networks were visualized using igraph.

### 3. Results

We found that individual sociality was consistent; beetles maintained their level of social interaction in experimental

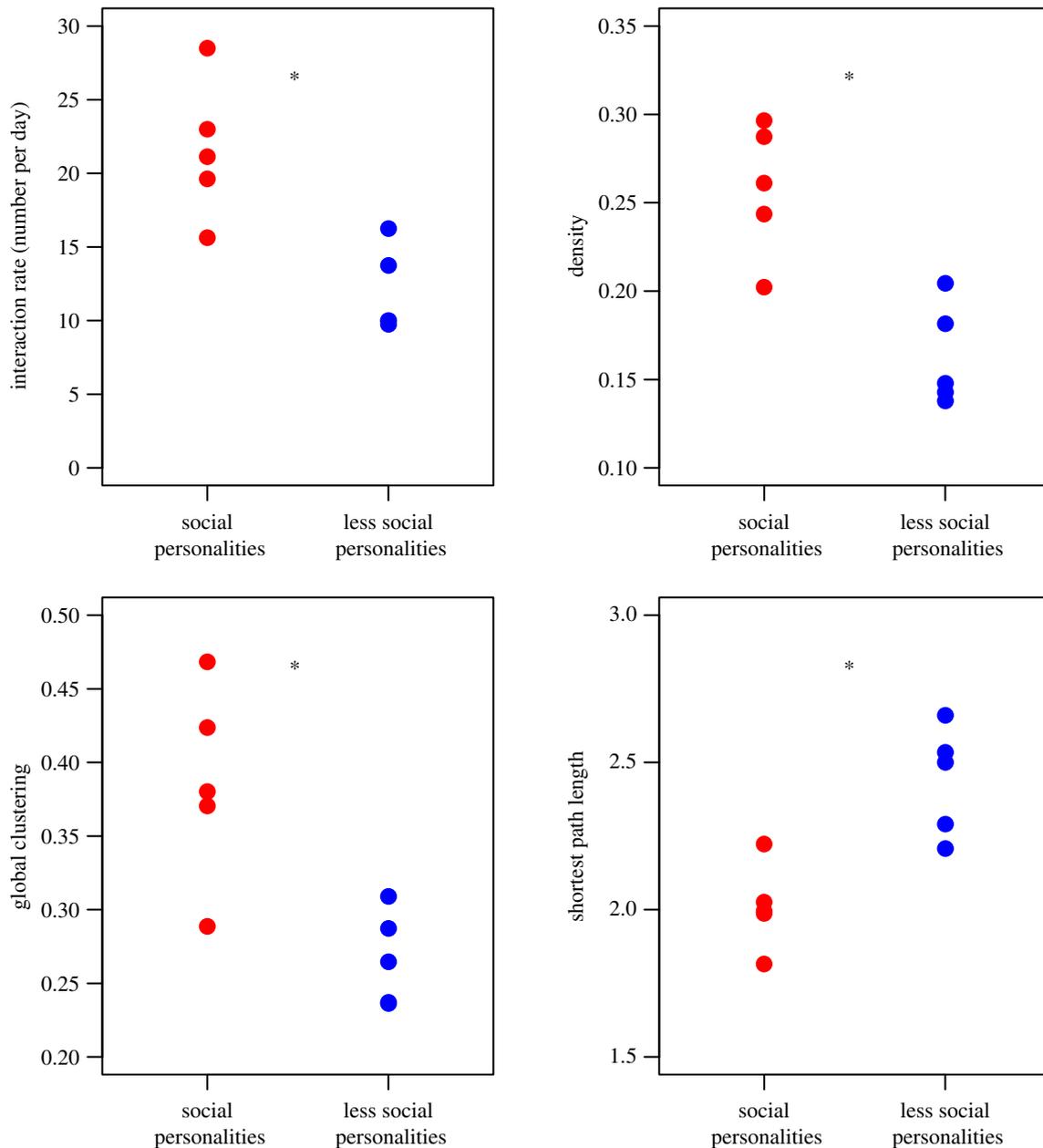
populations with new partners. Both number of interactions and number of social partners, or network degree, were repeatable (interactions:  $r = 0.34$ , 95% CrI = 0.23–0.43; partners:  $r = 0.39$ , 95% CrI = 0.32–0.50). Both observed repeatabilities were significantly greater than those calculated from permuted datasets, whether we shuffled within or across treatments (interactions:  $p < 0.001$ , partners:  $p < 0.001$ ).

Social network structure depended on the individual social traits within the group (figure 1). Networks composed of beetles who had been highly social in their previous social context had more interactions per day (mean difference = 9.6, 95% CI = 3.7–15.6,  $p < 0.01$ ), a higher density of ties (mean = 0.09, 95% CI = 0.05–0.14,  $p < 0.01$ ), higher global clustering (mean = 0.12, 95% CI = 0.04–0.20,  $p < 0.01$ ) and shorter average path lengths (mean =  $-0.44$ , 95% CI =  $-0.67$ – $-0.18$ ,  $p = 0.002$ ) than those composed of previously less social beetles (figure 2).

### 4. Discussion

We found that group social networks differed dramatically depending on the personalities of their members. By experimentally engineering groups comprised individuals with divergent levels of sociality, we showed that assemblages of highly social individuals interacted frequently and broadly, created densely connected networks with high clustering and short network distances between individuals. Conversely, groups composed of individuals who were less social in previous networks exhibited sparse networks with fewer closed triads and long paths. Individual beetles expressed consistent social tendencies even in a new social environment. These results suggest individuals in this non-eusocial insect system have social personalities, that these personalities shape group social structures, and that any process that causes the composition of personalities to vary among groups—such as a relationship between sociality and dispersal [83,84]—could produce variation in group structure.

Two measures of sociality, number of interactions and number of partners, had repeatability values comparable to those of other behavioural traits in this species and others



**Figure 2.** Four metrics of group network structure for the 10 experimental populations. Each point represents one population. Statistically significant differences between the treatments are indicated by asterisks.

[63,73,85]. Our results add to an increasing body of work on sociability as a personality trait [55]. From a network perspective, these results suggest that variation in individual behaviour is a predictor of social structures, but we note that there is still room for social environments to shape individual behaviour and potentially create feedbacks [30].

The differences in network structure generated by group composition may have implications for the transmission of information [6,86] and pathogens [87] through populations. One notable result is that no completely isolated nodes were found in the groups of more social individuals. Isolated individuals have lower exposure to aggression and diseases transmitted through contact, but also fewer interactions with potential mates. These impacts illustrate that both the benefits and costs of social interaction experienced by individuals will depend on the personalities of the conspecifics around them. Future work could test whether the composition of personalities within a group affects processes such as the rate of disease spread.

Variation in group composition can produce variation in group-level characters, which can in turn impact individual fitness [30,88]. *B. cornutus* females in populations with higher tie densities lay fewer eggs than those in sparsely connected populations [40]. Our results show that tie density can be impacted by the personality composition of the group, meaning that one source of variance in female fitness could be the personalities of her fellow group members. Females could therefore increase their fitness by avoiding groups of highly social individuals.

A field study found that selection on social network position was highly variable among populations of *B. cornutus*. Selection on individual strength, a metric combining the two behaviours measured in this study, trended more positively in populations with higher tie density [19]. Further data are needed to confirm whether this relationship is causal. But if network structure alters patterns of selection, populations composed of individuals with more social personalities might create environments in which being social

is favoured, potentially creating feedback loops driving the evolution of social personality types [88].

Our results suggest that network structures could evolve through changing group composition across generations. In the absence of a group-level method of replication, the evolution of a group trait can be understood as the evolution of underlying individual traits [89,90]. A recent meta-analysis found that affiliative social behaviours were moderately heritable [91], a few studies have found a genetic basis of individual social network position [92–95], and indirect genetic pathways can provide additional heritable variation [96–99]. Therefore, social personality types can change in frequency in response to selection. The evolution of social behaviours, whose expression in one individual may alter their expression in its partners, may be especially rapid [96,100–104]. We have shown that shifting the composition of individual traits in a group changes group traits within a generation. This experimental result demonstrates a causal link between individual personality and group phenotypes that could help explain how the social structures of animal societies evolve.

**Data accessibility.** Datasets of individual and group metrics, along with the code for statistical analyses, are available from the

Dryad Digital Repository: <https://doi.org/10.5061/dryad.0rxwdb24> [105].

**Authors' contributions.** P.A.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, visualization, writing—original draft and writing—review and editing; O.M.B.: conceptualization, data curation, funding acquisition, investigation and writing—original draft; R.A.C.: conceptualization, data curation, methodology, project administration, software and writing—review and editing; V.A.F.: conceptualization, funding acquisition, methodology, software, supervision and writing—review and editing; E.D.B.III.: conceptualization, funding acquisition, methodology, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Competing interests.** We declare we have no competing interests.

**Funding.** Funding for this work was provided by an NSF GRF to P.A.C., a University of Virginia award to P.A.C. and O.M.B., NSF IOS-1355029 to V.A.F. and IOS-1355003 and DEB-1911485 to E.D.B.III, and NSF REU grant no. 1461169 to Mountain Lake Biological Station.

**Acknowledgements.** We thank Eileen Butterfield, Liza Mitchem, Malcolm Augat, Catherine Debban and Fisher Brodie for construction; Hannah Donald, Savanna Cabrera, Olivia Shaffer and Molly Sayles for data collection; Liza Mitchem for statistical advice; Henry Wilbur for feedback; and the staff of Mountain Lake Biological Station for their support.

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