

Research



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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 fluorescent 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

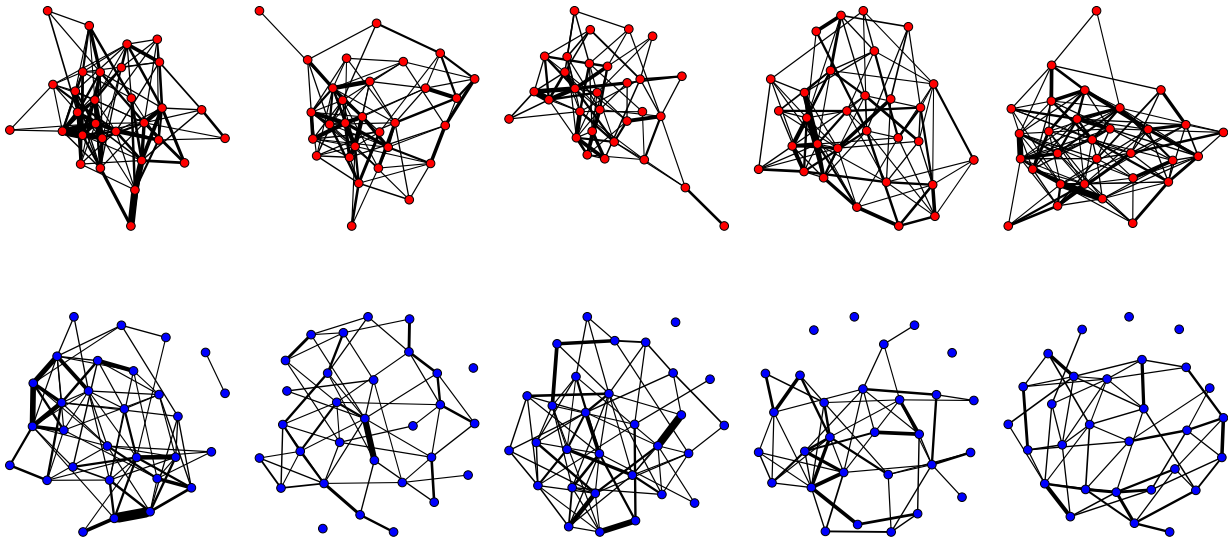


Figure 1. Networks from the 10 experimental populations. Networks composed of highly social individuals (red points) differ in number, thickness and distribution of ties from those networks composed of less social individuals (blue points). Line thickness is proportional to the simple ratio index, and 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

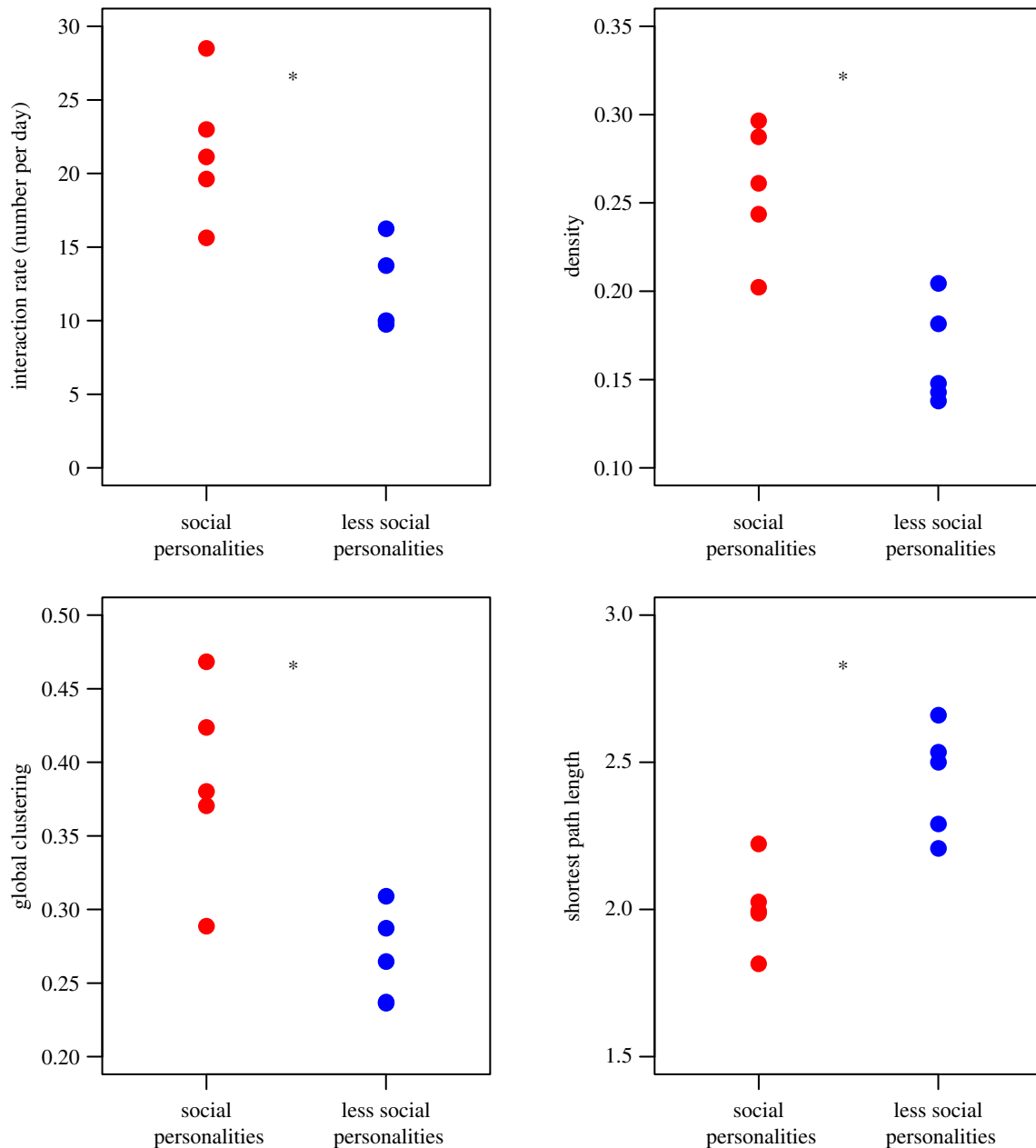


Figure 2. Four metrics of group network structure for the 10 experimental populations. Each point represents one population. Statistically significant differences between the treatments are indicated by asterisks.

[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.

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References

- Flack JC, Girvan M, deWaal FBM, Krakauer DC. 2006 Policing stabilizes construction of social niches in primates. *Nature* **439**, 426. (doi:10.1038/nature04326)
- Drewe JA. 2010 Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proc. R. Soc. B* **277**, 633–642. (doi:10.1098/rspb.2009.1775)
- Claidière N, Messer EJE, Hoppitt W, Whiten A. 2013 Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Curr. Biol.* **23**, 1251–1255. (doi:10.1016/j.cub.2013.05.036)
- Dey CJ, Reddon AR, O'Connor CM, Balshine S. 2013 Network structure is related to social conflict in a cooperatively breeding fish. *Anim. Behav.* **85**, 395–402. (doi:10.1016/j.anbehav.2012.11.012)
- VanderWaal KL, Atwill ER, Isbell LA, McCowan B. 2014 Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *J. Anim. Ecol.* **83**, 406–414. (doi:10.1111/1365-2656.12137)
- Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541. (doi:10.1038/nature13998)
- Carter GG, Farine DR, Crisp RJ, Vrtilek JK, Ripperger SP, Page RA. 2020 Development of new food-sharing relationships in vampire bats. *Curr. Biol.* **30**, 1275–1279. (doi:10.1016/j.cub.2020.01.055)
- Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234. (doi:10.1126/science.1088580)
- Ryder TB, McDonald DB, Blake JG, Parker PG, Loiselle BA. 2008 Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proc. R. Soc. B* **275**, 1367–1374. (doi:10.1098/rspb.2008.0205)
- Silk JB, Beehner JC, Bergman TJ, Crookford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B* **276**, 3099–3104. (doi:10.1098/rspb.2009.0681)
- Oh KP, Badyaev AV. 2010 Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *Am. Nat.* **176**, E80–E89. (doi:10.1086/655216)
- Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. *Curr. Biol.* **20**, 2207–2210. (doi:10.1016/j.cub.2010.10.058)
- Barocas A, Ilany A, Koren L, Kam M, Geffen E. 2011 Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE* **6**, e22375. (doi:10.1371/journal.pone.0022375)
- Gilby IC, Brent LNJ, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, Pusey AE. 2013 Fitness benefits of coalitionary aggression in male chimpanzees. *Behav. Ecol. Sociobiol.* **67**, 373–381. (doi:10.1007/s00265-012-1457-6)
- Wey TW, Burger JR, Ebensperger LA, Hayes LD. 2013 Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Anim. Behav.* **85**, 1407–1414. (doi:10.1016/j.anbehav.2013.03.035)
- Bar Ziv E, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L. 2016 Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. *Behav. Ecol. Sociobiol.* **70**, 901–912. (doi:10.1007/s00265-016-2112-4)
- Cheney DL, Silk JB, Seyfarth RM. 2016 Network connections, dyadic bonds and fitness in wild female baboons. *R. Soc. Open Sci.* **3**, 160255. (doi:10.1098/rsos.160255)
- Yang WJ, Maldonado-Chaparro AA, Blumstein DT. 2017 A cost of being amicable in a hibernating mammal. *Behav. Ecol.* **28**, 11–19. (doi:10.1093/beheco/arw125)
- Formica V, Donald H, Marti H, Irgebay Z, Brodie E. 2021 Social network position experiences more variable selection than weaponry in wild subpopulations of forked fungus beetles. *J. Anim. Ecol.* **90**, 168–182. (doi:10.1111/1365-2656.13322)
- Bond ML, Lee DE, Farine DR, Ozgul A, König B. 2021 Sociability increases survival of adult female giraffes. *Proc. R. Soc. B* **288**, 20202770. (doi:10.1098/rspb.2020.2770)
- Jacoby DMP, Fear LN, Sims DW, Croft DP. 2014 Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behav. Ecol. Sociobiol.* **68**, 1995–2003. (doi:10.1007/s00265-014-1805-9)
- Krause S, Wilson ADM, Ramnarine IW, Herbert-Read JE, Clément RJG, Krause J. 2016 Guppies occupy consistent positions in social networks: mechanisms and consequences. *Behav. Ecol.* **28**, arw177. (doi:10.1093/beheco/arw177)
- Kulahci IG, Ghazanfar AA, Rubenstein DL. 2018 Consistent individual variation across interaction networks indicates social personalities in lemurs. *Anim. Behav.* **136**, 217–226. (doi:10.1016/j.anbehav.2017.11.012)
- O'Brien PP, Webber QMR, Wal EV. 2018 Consistent individual differences and population plasticity in network-derived sociality: an experimental

- manipulation of density in a gregarious ungulate. *PLoS ONE* **13**, e0193425. (doi:10.1371/journal.pone.0193425)
25. Jones TB, Evans JC, Morand FJ. 2019 Urbanization and the temporal patterns of social networks and group foraging behaviors. *Ecol. Evol.* **9**, 4589–4602. (doi:10.1002/ece3.5060)
 26. Blaszczyk MB. 2018 Consistency in social network position over changing environments in a seasonally breeding primate. *Behav. Ecol. Sociobiol.* **72**, 11. (doi:10.1007/s00265-017-2425-y)
 27. Strickland K, Frère CH. 2018 Predictable males and unpredictable females: repeatability of sociability in eastern water dragons. *Behav. Ecol.* **29**, 236–243. (doi:10.1093/beheco/axr148)
 28. Plaza M *et al.* 2020 Repeatable social network node-based metrics across populations and contexts in a passerine. *J. Evol. Biol.* **33**, 1634–1642. (doi:10.1111/jeb.13703)
 29. Pinter-Wollman N *et al.* 2014 The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255. (doi:10.1093/beheco/art047)
 30. Cantor M *et al.* 2021 The importance of individual-to-society feedbacks in animal ecology and evolution. *J. Anim. Ecol.* **90**, 27–44. (doi:10.1111/1365-2656.13336)
 31. Ilany A. 2020 Complex societies, simple processes: a comment on Shizuka and Johnson. *Behav. Ecol.* **31**, 13. (doi:10.1093/beheco/arz107)
 32. Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014 The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* **29**, 326–335. (doi:10.1016/j.tree.2014.04.002)
 33. Bailey NW, Moore AJ. 2018 Evolutionary consequences of social isolation. *Trends Ecol. Evol.* **33**, 595–607. (doi:10.1016/j.tree.2018.05.008)
 34. Gordon DM. 1996 The organization of work in social insect colonies. *Nature* **380**, 121–124. (doi:10.1038/380121a0)
 35. Nandi AK, Sumana A, Bhattacharya K. 2014 Social insect colony as a biological regulatory system: modelling information flow in dominance networks. *J. R. Soc. Interface* **11**, 20140951. (doi:10.1098/rsif.2014.0951)
 36. Reia SM, Fontanari JF. 2017 Effect of group organization on the performance of cooperative processes. *Ecol. Complexity* **30**, 47–56. (doi:10.1016/j.ecocom.2016.09.002)
 37. Royle NJ, Pike TW, Heeb P, Richner H, Kölliker M. 2012 Offspring social network structure predicts fitness in families. *Proc. R. Soc. B* **279**, 4914–4922. (doi:10.1098/rspb.2012.1701)
 38. Solomon-Lane TK, Pradhan DS, Willis MC, Grober MS. 2015 Agonistic reciprocity is associated with reduced male reproductive success within harem social networks. *Proc. R. Soc. B* **282**, 20150914. (doi:10.1098/rspb.2015.0914)
 39. Stroeymeyt N, Grasse AV, Crespi A, Mersch DP, Cremer S, Keller L. 2018 Social network plasticity decreases disease transmission in a eusocial insect. *Science* **362**, 941–945. (doi:10.1126/science.aat4793)
 40. Costello R. 2020 *The ecological causes and adaptive consequences of social behaviors in forked fungus beetles (Bolitotherus cornutus)*. Charlottesville, VA: University of Virginia.
 41. Godfrey SS, Sih A, Bull CM. 2013 The response of a sleepy lizard social network to altered ecological conditions. *Anim. Behav.* **86**, 763–772. (doi:10.1016/j.anbehav.2013.07.016)
 42. Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE. 2014 Across-year social stability shapes network structure in wintering migrant sparrows. *Ecol. Lett.* **17**, 998–1007. (doi:10.1111/ele.12304)
 43. Wilson ADM, Krause S, James R, Croft DP, Ramnarine IW, Borner KK, Clement RJG, Krause J. 2014 Dynamic social networks in guppies (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **68**, 915–925. (doi:10.1007/s00265-014-1704-0)
 44. Wilson ADM, Krause S, Ramnarine IW, Borner KK, Clément RJG, Kurvers RHJM, Krause J. 2015 Social networks in changing environments. *Behav. Ecol. Sociobiol.* **69**, 1617–1629. (doi:10.1007/s00265-015-1973-2)
 45. Aplin LM *et al.* 2015 Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Anim. Behav.* **108**, 117–127. (doi:10.1016/j.anbehav.2015.07.016)
 46. Sih A, Watters JV. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour* **142**, 1417–1431. (doi:10.1163/156853905774539454)
 47. Laskowski KL, Bell AM. 2014 Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. *Anim. Behav.* **90**, 287–295. (doi:10.1016/j.anbehav.2014.02.010)
 48. Jolles JW, Boogert NJ, Sridhar VH, Couzin ID, Manica A. 2017 Consistent individual differences drive collective behavior and group functioning of schooling fish. *Curr. Biol.* **27**, 2862–2868. (doi:10.1016/j.cub.2017.08.004)
 49. Keiser CN, Pruitt JN. 2014 Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proc. R. Soc. B* **281**, 20141424. (doi:10.1098/rspb.2014.1424)
 50. Pinter-Wollman N, Mi B, Pruitt JN. 2017 Replacing bold individuals has a smaller impact on group performance than replacing shy individuals. *Behav. Ecol.* **28**, 883–889. (doi:10.1093/beheco/axr054)
 51. Montiglio P-O, Wey TW, Sih A. 2017 Effects of the group's mix of sizes and personalities on the emergence of alternative mating systems in water striders. *Behav. Ecol.* **28**, 1068–1074. (doi:10.1093/beheco/axr070)
 52. Hillesheim E, Koeniger N, Moritz RFA. 1989 Colony performance in honeybees (*Apis mellifera capensis* Esch.) depends on the proportion of subordinate and dominant workers. *Behav. Ecol. Sociobiol.* **24**, 291–296. (doi:10.1007/BF00290905)
 53. Pike TW, Madhumita S, Jan L, Nick JR. 2008 Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B* **275**, 2515–2520. (doi:10.1098/rspb.2008.0744)
 54. Dakin R, Moore IT, Horton BM, Vernasco BJ, Ryder TB. 2021 Testosterone-mediated behaviour shapes the emergent properties of social networks. *J. Anim. Ecol.* **90**, 131–142. (doi:10.1111/1365-2656.13305)
 55. Gartland LA, Firth JA, Laskowski KL, Jeanson R, Ioannou CC. 2021 Sociability as a personality trait in animals: methods, causes and consequences. *Biol. Rev.* (doi:10.1111/brv.12823)
 56. Krause J, James R, Croft DP. 2010 Personality in the context of social networks. *Phil. Trans. R. Soc. B* **365**, 4099–4106. (doi:10.1098/rstb.2010.0216)
 57. Bergmüller R, Taborsky M. 2010 Animal personality due to social niche specialisation. *Trends Ecol. Evol.* **25**, 504–511. (doi:10.1016/j.tree.2010.06.012)
 58. Montiglio PO, Ferrari C, Réale D. 2013 Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Phil. Trans. R. Soc. B* **368**, 20120343. (doi:10.1098/rstb.2012.0343)
 59. Smith LA, Swain DL, Innocent GT, Nevison I, Hutchings MR. 2019 Considering appropriate replication in the design of animal social network studies. *Sci. Rep.* **9**, 7208. (doi:10.1038/s41598-019-43764-9)
 60. Farine DR, Aplin LM. 2019 Spurious inference when comparing networks. *Proc. Natl Acad. Sci. USA* **116**, 16 674–16 675. (doi:10.1073/pnas.1900143116)
 61. Liles MP. 1956 A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). *Ohio J. Sci.* **56**, 329–337.
 62. Pace A. 1967 Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). *Occasional Papers Mus. Zool.* **653**, 1–15.
 63. Formica V, Wood C, Cook P, Brodie III ED. 2017 Consistency of animal social networks after disturbance. *Behav. Ecol.* **28**, 85–93. (doi:10.1093/beheco/arw128)
 64. Formica V, Wood C, Larsen W, Butterfield R, Augat M, Hougen H, Brodie III E. 2012 Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). *J. Evol. Biol.* **25**, 130–137. (doi:10.1111/j.1420-9101.2011.02411.x)
 65. Abramoff M, Magalhães P, Ram SJ. 2003 Image processing with ImageJ. *Biophotonics Int.* **11**, 36–42.
 66. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267. (doi:10.1163/156853974X00534)
 67. Whitehead H, Dufault S. 1999 Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. In *Advances in the study of behavior* (eds PJB Slater, JS Rosenblat, CT Snowden, TJ Roper), pp. 33–74. New York, NY: Academic Press.
 68. Davis GH, Crofoot MC, Farine DR. 2018 Estimating the robustness and uncertainty of animal social networks using different observational methods. *Anim. Behav.* **141**, 29–44. (doi:10.1016/j.anbehav.2018.04.012)

69. Falconer D, Mackay T. 1996 *Introduction to quantitative genetics*. Essex, UK: Longman.
70. Nakagawa S, Schielzeth H. 2010 Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev.* **85**, 935–956. (doi:10.1111/j.1469-185X.2010.00141.x)
71. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Softw.* **33**, 1–22. (doi:10.18637/jss.v033.i02)
72. Hadfield J. 2014 MCMCglmm Course Notes. See <https://mran.microsoft.com/snapshot/2018-03-30/web/packages/MCMCglmm/vignettes/CourseNotes.pdf>.
73. Bell AM, Hankison SJ, Laskowski KL. 2009 The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**, 771–783. (doi:10.1016/j.anbehav.2008.12.022)
74. Farine DR, Carter GG. 2021 Permutation tests for hypothesis testing with animal social network data: problems and potential solutions. *Methods Ecol. Evol.* **13**, 144–156. (doi:10.1111/2041-210X.13741)
75. Hart JDA, Weiss MN, Brent LNJ, Franks DW. 2021 Common permutation methods in animal social network analysis do not control for non-independence., 2021.06.04.447124. (doi:10.1101/2021.06.04.447124)
76. Ginsberg JR, Young TP. 1992 Measuring association between individuals or groups in behavioural studies. *Anim. Behav.* **44**, 377–379. (doi:10.1016/0003-3472(92)90042-8)
77. Whitehead H. 2008 Precision and power in the analysis of social structure using associations. *Anim. Behav.* **75**, 1093–1099. (doi:10.1016/j.anbehav.2007.08.022)
78. James R, Croft DP, Krause J. 2009 Potential banana skins in animal social network analysis. *Behav. Ecol. Sociobiol.* **63**, 989–997. (doi:10.1007/s00265-009-0742-5)
79. Croft DP, Madden JR, Franks DW, James R. 2011 Hypothesis testing in animal social networks. *Trends Ecol. Evol.* **26**, 502–507. (doi:10.1016/j.tree.2011.05.012)
80. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
81. Opsahl T. 2009 *Structure and evolution of weighted networks*. London, UK: University of London Queen Mary College. See <http://toreopsahl.com/publications/thesis/>.
82. Opsahl T, Panzarasa P. 2009 Clustering in weighted networks. *Soc. Netw.* **31**, 155–163. (doi:10.1016/j.socnet.2009.02.002)
83. Cote J, Clibert J. 2007 Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. B* **274**, 383–390. (doi:10.1098/rspb.2006.3734)
84. Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A. 2010 Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc. R. Soc. B* **277**, 1571–1579. (doi:10.1098/rspb.2009.2128)
85. Mitchem LD, Debray R, Formica VA, Brodie III ED. 2019 Contest interactions and outcomes: relative body size and aggression independently predict contest status. *Anim. Behav.* **157**, 43–49. (doi:10.1016/j.anbehav.2019.06.031)
86. Allen J, Weinrich M, Hoppitt W, Rendell L. 2013 Network-based diffusion analysis reveals cultural transmission of Lobtail feeding in humpback whales. *Science* **340**, 485–488. (doi:10.1126/science.1231976)
87. Keeling MJ, Eames KTD. 2005 Networks and epidemic models. *J. R. Soc. Interface* **2**, 295–307. (doi:10.1098/rsif.2005.0051)
88. Farine DR, Montiglio PO, Spiegel O. 2015 From individuals to groups and back: the evolutionary implications of group phenotypic composition. *Trends Ecol. Evol.* **30**, 609–621. (doi:10.1016/j.tree.2015.07.005)
89. Okasha S. 2014 Emergent group traits, reproduction, and levels of selection: commentary on P. Smaldino. *Behav. Brain Sci.* **37**, 268–269. (doi:10.1017/S0140525X13002963)
90. Sueur C, Romano V, Sosa S, Puga-Gonzalez I. 2019 Mechanisms of network evolution: a focus on socioecological factors, intermediary mechanisms, and selection pressures. *Primates* **60**, 167–181. (doi:10.1007/s10329-018-0682-7)
91. Dochtermann NA, Schwab T, Anderson Berdal M, Dalos J, Royauté R. 2019 The heritability of behavior: a meta-analysis. *J. Heredity* **110**, 403–410. (doi:10.1093/jhered/esz023)
92. Fowler JH, Dawes CT, Christakis NA. 2009 Model of genetic variation in human social networks. *Proc. Natl Acad. Sci. USA* **106**, 1720–1724. (doi:10.1073/pnas.0806746106)
93. Lea AJ, Blumstein DT, Wey TW, Martin JGA. 2010 Heritable victimization and the benefits of agonistic relationships. *Proc. Natl Acad. Sci. USA* **107**, 21 587–21 592. (doi:10.1073/pnas.1009882107)
94. Brent LNJ, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson AG, Skene JHP, Platt ML. 2013 Genetic origins of social networks in rhesus macaques. *Sci. Rep.* **3**, 1042. (doi:10.1038/srep01042)
95. Wice EW, Saltz JB. 2021 Selection on heritable social network positions is context-dependent in *Drosophila melanogaster*. *Nat. Commun.* **12**, 3357. (doi:10.1038/s41467-021-23672-1)
96. Moore AJ, Brodie III ED, Wolf JB. 1997 Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution* **51**, 1352–1362. (doi:10.2307/2411187)
97. Wolf JB, Brodie III ED, Cheverud JM, Moore AJ, Wade MJ. 1998 Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* **13**, 64–69. (doi:10.1016/S0169-5347(97)01233-0)
98. McGlothlin JW, Brodie III ED. 2009 How to measure indirect genetic effects: the congruence of trait-based and variance-partitioning approaches. *Evolution* **63**, 1785–1795. (doi:10.1111/j.1558-5646.2009.00676.x)
99. Fisher DN, McAdam AG. 2017 Social traits, social networks and evolutionary biology. *J. Evol. Biol.* **30**, 2088–2103. (doi:10.1111/jeb.13195)
100. Bleakley BH, Brodie III ED. 2009 Indirect genetic effects influence antipredator behavior in guppies: estimates of the coefficient of interaction Ψ and the inheritance of reciprocity. *Evolution* **63**, 1796–1806. (doi:10.1111/j.1558-5646.2009.00672.x)
101. Wilson AJ, Morrissey MB, Adams MJ, Walling CA, Guinness FE, Pemberton JM, Clutton-Brock TH, Kruuk LEB. 2011 Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. *J. Evol. Biol.* **24**, 772–783. (doi:10.1111/j.1420-9101.2010.02212.x)
102. Franz M, McLean E, Tung J, Altmann J, Alberts SC. 2015 Self-organizing dominance hierarchies in a wild primate population. *Proc. R. Soc. B* **282**, 20151512. (doi:10.1098/rspb.2015.1512)
103. Santostefano F, Wilson AJ, Araya-Ajoy YG, Dingemans NJ. 2016 Interacting with the enemy: indirect effects of personality on conspecific aggression in crickets. *Behav. Ecol.* **27**, 1235–1246. (doi:10.1093/beheco/arw037)
104. Brask JB *et al.* 2019 Evolution of non-kin cooperation: social assortment by cooperative phenotype in guppies. *R. Soc. Open Sci.* **6**, 181493. (doi:10.1098/rsos.181493)
105. Cook PA, Baker OM, Costello RA, Formica VA, Brodie III ED. 2022 Data from: Group composition of individual personalities alters social network structure in experimental populations of forked fungus beetles. Dryad Digital Repository. (doi:10.5061/dryad.0rxwdb24)